

**Anatomical and Physiological Comparisons Between the Dorsal and
Ventral Regions of the Lateral Geniculate Nucleus in Mice**

NEUR 494 Honors Thesis
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Abstract

Our overall goal is to understand how the lateral geniculate nucleus (LGN) of the thalamus transforms information it receives from the retina. The LGN encompasses a dorsal and a ventral subnucleus; each of which receives retinotopically organized input from ganglion cells. The dorsal lateral geniculate nucleus (dLGN) supplies the main input to visual cortex and is associated with form vision. The dLGN has been studied intensively. The ventral lateral geniculate nucleus (vLGN) projects to subcortical structures involved with motor tasks. At present, very little is known about the anatomy and physiology of single cells in this structure. We began to explore the functional role of the vLGN by comparing the size and structure of receptive fields there to those recorded from the dLGN. The receptive fields in the vLGN were far larger than those in the LGN. We hypothesized that this disparity in size might reflect differences in the extent of dendritic arbors in the ventral vs. dorsal divisions of the nucleus. Indeed, we found that the spatial extents of dendritic arbors in the vLGN were far larger than those in the dLGN, often spanning the width or height of the nucleus. This is consistent with the idea that the large receptive fields in the vLGN are formed by convergent input from ganglion cells that represent disparate regions of visual space. Additional physiological analyses support this view. All told, it is possible that inputs from the vLGN convey information from large regions of visual space and helps to coordinate or modulate the activity of groups of cells in downstream targets.

Introduction

Our overall goal is to understand how the visual thalamus transforms information it receives from the retina. The visual portion of the thalamus, the lateral geniculate nucleus (LGN) comprises two main divisions, each of which receives retinotopically organized input from ganglion cells. The dorsal lateral geniculate nucleus (dLGN) provides the main input to visual cortex and is associated with form vision (Dhande and Huberman, 2014). The ventral lateral geniculate nucleus (vLGN) projects to subcortical structures involved with motor tasks (Harrington 1997), where it exerts an inhibitory influence (Golding et al., 2014). At present, very little is known about the anatomy and physiology of single cells in the vLGN.

Previous studies of the vLGN *in vivo* had been limited to qualitative accounts of the receptive field size and sign (Harrington 1997, Spear et al., 1997, & Sumitomo et al., 1979), with reports that cells there prefer bright (On) to dark (Off) stimuli and have large receptive fields (Harrington 1997, Sumitomo 1979, & Spear 1977). Anatomical studies provided partial reconstructions of the dendritic arbors of cells in the vLGN and showed that some neurons had long dendrites.

In higher mammals, the vLGN is much smaller than the dLGN (Harrington 1997), making it harder to access *in vivo*. However, in rodents, the vLGN is relatively large, providing opportunities to study this structure *in situ* (Harrington 1997). We took advantage of this species difference to explore the visual processing in the vLGN. We made whole-cell recordings using dye-filled pipettes from neurons in the vLGN during visual stimulation. Thus we were able to characterize the anatomy of neurons whose receptive fields and response properties had been assessed *in vivo* (Ciftcioglu et al., 2014, 2015). We compared these analyses to previous observations our laboratory had made about relay cells in the dLGN. Our specific focus was to explore relationships between the spatial extent of the dendritic arbor and physiological properties such as receptive field size and mechanisms of synaptic integration for each division of the LGN.

Our results show, quantitatively, that receptive fields of cells in the vLGN are much larger than those in the dLGN, and that this disparity is paralleled by differences in the spatial extent of the dendritic arbors in the two subnuclei. In fact the dendritic arbors of most cells in the vLGN were so wide they reached from one pole of the structure to the other, integrating large regions of visual space. By contrast dendritic arbors in the dLGN were compact, as had been noted by others (and see Krahe et al. 2011). Further, we compared the shape of the intracellular signals recorded from neurons in the two divisions of the LGN. Large unitary retinogeniculate excitatory postsynaptic potentials (EPSCs) were prominent in recordings from the dLGN whereas individual EPSCs were small and often difficult to resolve in traces from the vLGN. Taken together, our results are consistent with the view the large receptive fields of cells in the vLGN are constructed from small contributions of many ganglion cells.

Methods

Preparation: Adult, pigmented (C57BL/6) mice were sedated with chlorproxithene (5mg/kg) and then anesthetized with urethane (0.5-1 g/kg 10% w/v in saline, i.p.) (Neill and Stryker, 2008). Body temperature was measured using a rectal probe and maintained at 36.7°C with a heating blanket. After retracting the scalp, a small headpost was affixed to the skull and a small craniotomy centered around the location of the LGN was made. The dura was left intact to prevent rupturing of blood vessels on the surface of the brain. All procedures were in accordance with the guidelines of the US National Institute of Health and the Institutional Animal Care and Use Committees of the University of Southern California.

Recordings: Whole-cell recordings with biocytin-filled pipettes were made using standard techniques (Hirsch et al., 1998). Pipette resistances, measured from responses to current injections, varied between 5-20 Mohms. Neural data was recorded with an Axopatch 200A amplifier (Axon instruments), digitized at 10KHz (Power 1401 data acquisition system, Cambridge Electronic Design) and stored for further analysis. We did not assign absolute resting voltage, because the ratio of the access to seal resistance lead to voltage division of the neural signal.

Stimulation: Our stimulus was sparse noise (bright and dark spots (spot size: 2°-20°)) displayed in pseudo random order, 16 times each on a 16x16 grid (Jones and Palmer, 1987). Stimuli parameters were adjusted to evoke maximum spiking response from the cell. Stimuli were presented at 35 frames per second on a gamma corrected Dell 2211H monitor (refresh rate=70Hz) using a stimulus generator (ViSaGe, Cambridge Research Ltd.). The monitor was positioned between 150-180mm in front of the animal.

Detecting Spikes and EPSCs: We developed an algorithm to detect EPSCs and spikes from intracellular recordings using a support vector machine (SVM) {Chang, 2011}. To detect potential neural events, we computed the first derivative of the intracellular signal and then applied a low threshold. At this stage, the detected data included both true events (EPSCs and spikes) and noise. Further sorting of the data was done using the SVM.

Histology and Anatomical analysis: At the end of the experiment, the animals were overdosed with isoflurane and perfused with 3% paraformaldehyde. The brains were removed and cut coronally into 100 μ m sections and then stained for biocytin (Hirsch et al., 1998). Cells were reconstructed in three dimensions using Neurolucida system (MicroBrightfield). Sholl analysis (Sholl et al, 1953) and convex hull analysis available in Neurolucida software were conducted to quantify dendritic arbor extent and volume, respectively.

Results

We performed *in vivo* whole cell recordings with dye-filled electrodes from the vLGN and associated intrageniculate leaflet (IGL) of adult mice during visual stimulation. Our sample includes 9 cells, 7 of which were well filled with dye (6 in the vLGN and 1 in the IGL). We compared this set of cells to 7, randomly chosen, relay cells in the dLGN that were part of a separate study.

Receptive fields of cells in the vLGN and IGL.

Past extracellular studies in the vLGN in cat (Spear et al., 1977) and rat (Sumitomo et al., 1979) described neural receptive fields as large and undifferentiated. By contrast, receptive fields of dLGN cells in these species are much smaller (Spear et al., 1977; Sumitomo et al., 1979). We asked whether this difference in receptive field size in the two divisions of the LGN is preserved in the mouse.

Our first goal was to map receptive fields in the vLGN (and IGL) and quantitatively compare these to those in the dLGN. The stimulus we chose was sparse noise, individually flashed bright and dark spots displayed on a grey background in pseudo random order. The receptive fields of two example cells in the vLGN (Figure 1A) are shown next to those of two randomly selected relay cells in dLGN (Figure 1D). Unlike the dLGN, where relay cells often have receptive fields with a center-surround structure, cells in the vLGN usually have large diffuse receptive fields. Of the 6 cells we analyzed, 4 were ON cells and 2 were OFF cells. A summary plot of sizes (determined with a 2D Gaussian fit) for 6 receptive fields in vLGN/IGL and dLGN is shown in Figure 1C. We next investigated the anatomical basis for the large receptive fields in the vLGN.

Figure 1: Receptive Fields in the vLGN and IGL are Large Compared to Those in the dLGN

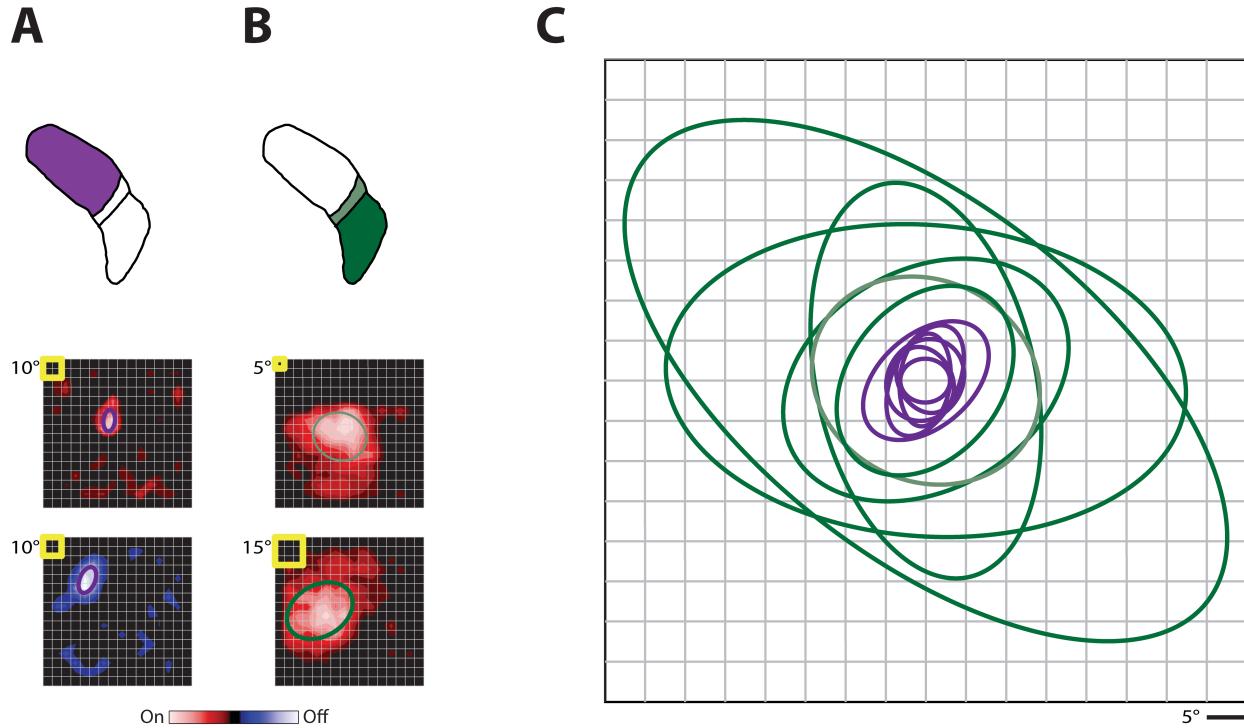


Figure 1. Receptive Fields in the vLGN/iGL are larger than those in the dLGN

(A)

Receptive fields of two ON cells in the vLGN/IGL mapped with flashed bright spots. (B) Receptive field of an ON-center relay cell (top) and an OFF center relay cell (bottom) in the dLGN mapped with sparse noise. Oval overlays are 1 sigma contours from 2D Gaussian fits of the receptive fields. Grid spacing spots is 5 degrees and spot size is indicated by the yellow squares. (C) Plots of the 1σ contours fit to the receptive field fits of the cells in the vLGN/IGL (green) and the relay cells in the dLGN (purple). The peak of each receptive field fit is aligned to the center of the stimulus grid; n=6 for both the vLGN/IGL and the dLGN.

Anatomical characteristics of vLGN cells compared to dLGN cells

In mouse, both dorsal and ventral LGN receive input from many populations of retinal ganglion cells and there is a retinotopic map of visual space in both nuclei. However, the receptive fields of cells in the vLGN cells are larger than those of presynaptic retinal ganglion cells (Dhande and Huberman, 2014; Sanes and Masland, 2015). How then do the differences in the receptive field sizes of cells in the two subnuclei emerge?

One possible reason for this difference is retinothalamic convergence ratios; cells with larger versus smaller receptive fields might receive more rather than fewer retinal inputs. High convergence can be achieved in different ways: (1) retinal axons could traverse large distances to synapse onto single vLGN cells with spatially confined dendritic arbors, (2) the dendrites of vLGN cells could extend over larger areas to reach remote retinal inputs, or (3) both the dendritic

arbors of relay cells and the terminal fields of retinal inputs might have large extents. Previous studies have shown that the retinal arbors are spatially restricted in the LGN (Sretavan D.W. and Shatz C.J., 1986, Hong et al., 2014). Thus, we predicted that the dendritic arbors of cells in the vLGN would extend for long distances, to integrate inputs across the retinotopic map.

To test this idea, we made computer assisted 3D reconstructions of the dendritic arbors for cells whose receptive fields had been mapped *in vivo*. Using commercial software (Neurolucida, MBFbioscience, Williston, VT) we analyzed the volume and extent of dendritic arbors in both the vLGN and dLGN. We found that while dendrites of the dLGN cells were confined to a small region of the nucleus, dendritic arbors in the vLGN spanned long distances, often extending into adjacent structures.

Statistical analysis comparing dLGN and vLGN cells

To compare the extent of dendritic arbors in the vLGN versus the dLGN, we conducted a Sholl analysis (Sholl, 1953). This analysis gives insight into how densely a cell samples its environment. To conduct the analysis we placed concentric rings, centered on the soma, at 5 μ m step sizes on a shrinkage corrected, 2D projection of each dendritic arbor (Fig. 2). The Sholl analysis (Fig. 2) revealed that branching patterns were markedly different in both nuclei. Dendritic arbors in the vLGN (Figure 2A) extended farther than those in the dLGN (Figure 2B), as seen for examples of each type of cell (right panels) and plots of the number of intersections vs. distance from the soma (left panels). The average for each distribution, is plotted in Figure 2C, where dashed lines indicate the standard error (SE). The distributions were significantly different (vLGN: M= 154.8 μ , SE=5.76 μ ; dLGN: M= 57.6 μ , SE=0.47 μ , p<0.05).

Figure 2: Sholl Analysis Comparing dLGN and vLGN/iGL Morphology

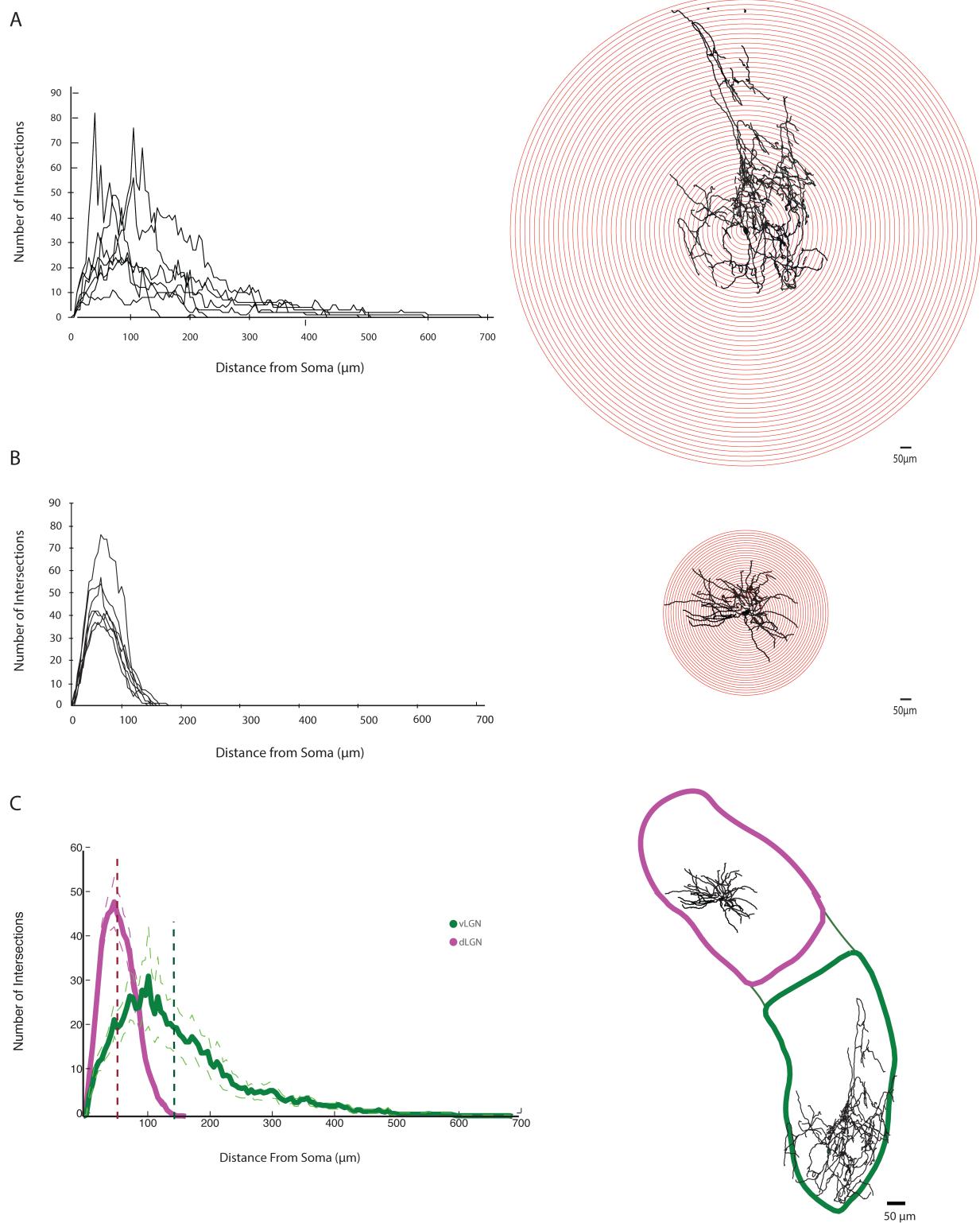
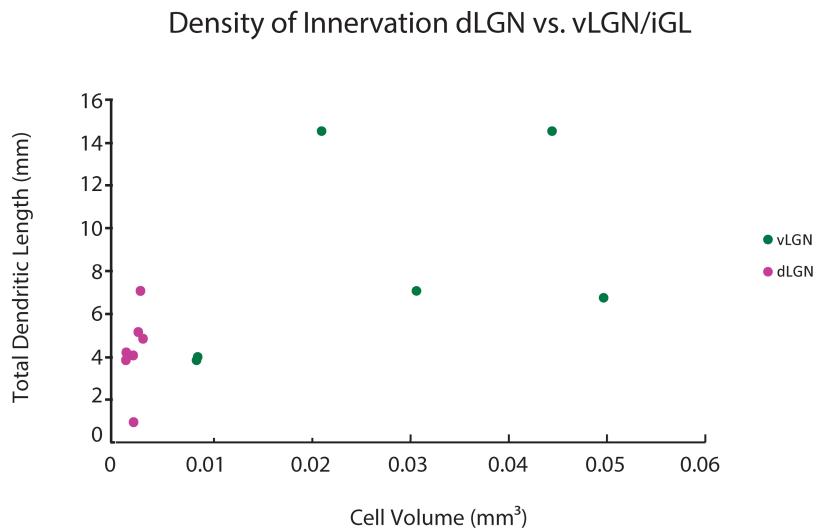


Figure 2. Sholl Analysis of the Dendritic Arbors of Cells in the dLGN and vLGN/IGL **(A)** Sholl analysis for the cells in the vLGN/IGL (left) and Sholl circles for a fully reconstructed sample cell (right). Each curve represents the number of intersections on Sholl circles as a function of distance from the soma for a single cell (left). **(B)** Sholl

analysis for the relay cells in the dLGN (left) and Sholl circles for sample relay cell (right). **(C)** Averaged curve of Sholl analyses for cells in the vLGN/iGL (green) and in the dLGN (purple) (left); and icon depicting reconstructions of a sample cell in the vLGN/IGL (green) and a sample relay cell in the dLGN (purple) within nuclear borders(right). Thick curves and thin dashed curves represent the mean and standard error of the mean, respectively, for each subnucleus as a function of distance from the soma (left). The vertical dashed line represents the average distance of all intersections from the soma for each subdivision. n=6 for each subdivision of the LGN. Scale bars are 50 microns.

To estimate the density of sampling across both dLGN and vLGN cells, we calculated total dendritic length divided by the cell's volume (convex hull analysis), scatter plot, Figure 3. The average density of innervation was significantly higher ($p<0.05$) for dLGN (geometric mean (GM)= $1376.4/\text{mm}^2$, SEM= $(+563/\text{mm}^2)/(-400/\text{mm}^2)$) than for vLGN (GM= 326 mm^2 , SEM= $(+85/\text{mm}^2)/(-67/\text{mm}^2)$), Figure 3. This is consistent with results from the Sholl analysis, which indicated that dendritic arbors in the dLGN were fuller and more compact than those in the vLGN.

Figure 3: Density of Innervation is Higher in dLGN than vLGN



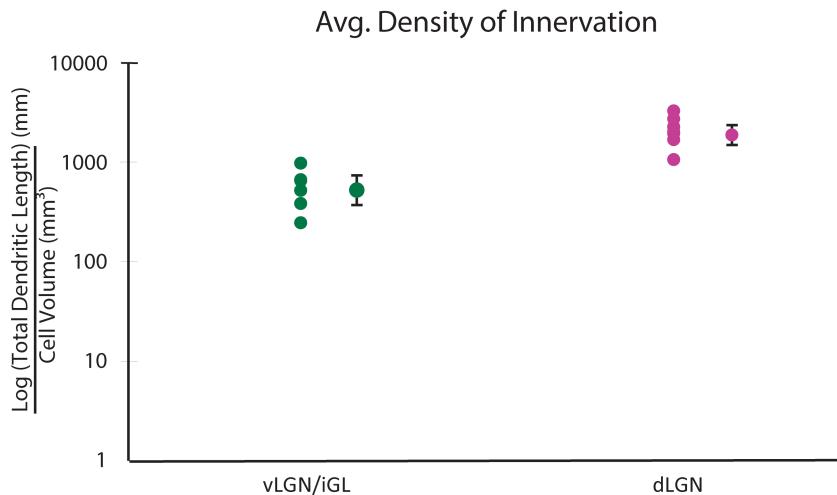


Figure 3. Dendritic Arbors are Sparse in VLGN/IGL and Dense in dLGN. (A) Total length of dendritic arbor and dendritic arbor volume for the cells in the vLGN/IGL (green) and the relay cells in the dLGN (purple). The volume of dendritic arbors in the vLGN/IGL is much larger than that for relay cells in the dLGN. (B) Average dendritic length per unit volume for the cells of the vLGN/IGL (green) and the relay cells in the dLGN (purple). The error bars represent the standard error of the mean; n=6 for each subdivision.

Relay cells in the cat's dLGN have been divided into X, Y and W categories based on physiological (Shapley and Hochstein, 1975, Wilson et al., 1976) and anatomical criteria (Sherman and Spear, 1982; Sherman, 1985). Most recently, in mouse, X-like (biconical), Y-like (symmetrical), and W-like (hemispheric) morphological profiles have been identified, based on the shape of the dendritic arbors (Krahe et al., 2011). To begin to explore shape of dendritic arbors in the vLGN, and to find out if they were quantitatively distinct from those in the dLGN, we developed a method to measure the isotropy of the dendritic arbors. For each cell, we measured the Euclidean distance from the soma to the end of the dendrite that extended the farthest from the soma. We then created a theoretical sphere around the soma, using this distance as the radius. Next, we calculated the ratio of the arbor volume (μm^3) to the volume of its theoretical sphere to generate an isotropism index (ISO*i*) (Figure 4). Thus, an index of 1.0 represents a cell with fully isotropic projections and small values indicate that the dendritic arbor extends farther in some directions than others. The resulting ISO*i* values between the dLGN and vLGN differed by an order of magnitude. Because the data was distributed exponentially, we calculated the geometric mean and standard error of the mean (vLGN: GM=0.055, SEM=0.075, 0.04; dLGN: GM=0.19, SEM=0.21, 0.18; p<0.05). This indicates that even as arbors extend for long distances in the vLGN, their projection patterns are not random or uniform.

Figure 4: The vLGN Has a Lower Index of Isotropism Than dLGN

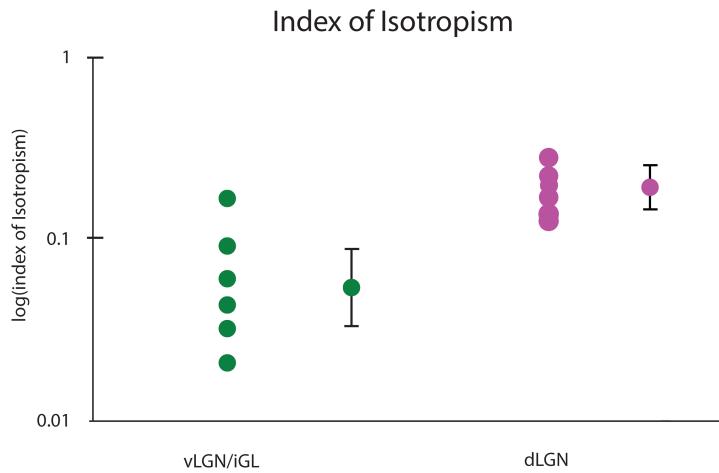


Figure 4. Cells the vLGN/IGL have Strongly Anisotropic Dendritic Arbors . (A) Index of Isotropism for cells in the vLGN/IGL (green) and relay cells in the dLGN (purple). The mean and standard error of the mean is plotted to the right side of points for individual cells; n=6 for each subdivision.

Different patterns of synaptic integration

The principle of synaptic scaling holds that as the number of presynaptic inputs a neuron integrates grown larger, the size of the synaptic potential that each input contributes grows smaller (Turrigiano, 2008). Relay cells in the dLGN receive only one to very few inputs and the EPSP each input generates is large. Thus it is not surprising that the dominant component of the intracellular waveform recorded from relay cells are large unitary EPSCs, Figure 5B. Past work from our laboratory quantified this observation using a deflection index (Wang et al., 2011) (Figure 5.) Such unitary inputs are rarely visible in recordings from the vLGN, as seen in the traces displayed in Figure 5A and in a plot that compares values for the deflection index in the two divisions of the LGN (Figure 5C). These results are consistent with the view that convergence values in the vLGN are higher than those in the dLGN.

Figure 5: Different Patterns of Synaptic Integration of the dLGN versus vLGN/iGL

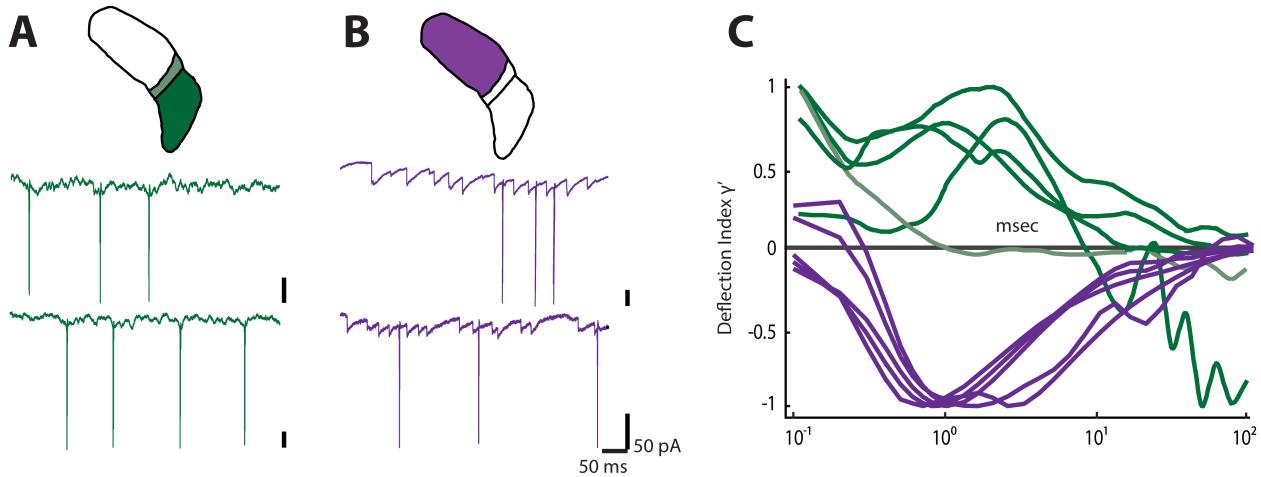


Figure 5. Analysis of Membrane Currents Recorded From the dLGN and vLGN/IGL (A) Sample membrane currents recorded from 2 cells in the vLGN/iGL (green) and (B) 2 relay cells in the dLGN (purple). Retinogeniculate EPSCs are visible clearly in the recordings of relay cells in the dLGN. By contrast, individual synaptic currents are rarely discernible in cells in the vLGN/IGL. (C) The shapes of membrane currents are quantified using the deflection index which reflects the relative weight of inward and outward currents at different timescales. Index values are negative when the membrane trajectory is depolarizing and vice versa. Plots of the deflection index across timescales for relay cells in the dLGN reflect the dominance of EPSCs whereas curves for the cells in the vLGN/IGL have no such trend; n=5 for each subdivision

Discussion

Summary

The dLGN is associated with form vision while the vLGN is thought to play role that does not depend on visual acuity. This view derives from past studies that suggested that receptive fields in the dLGN were smaller than those in the vLGN (Spear et al., 1977; Sumitomo et al., 1979), even though both subnuclei receive input from shared populations of ganglion cells (Ecker et al., 2010; Kay et al., 2011; Rivlin-Etzion et al., 2011). To explore the role of the vLGN further, we quantified the differences in receptive field size and synaptic physiology in the two divisions of the LGN and then explored potential anatomical bases for those differences. For example, we hypothesized that disparity in receptive field size between the two subnuclei might scale with the extent of dendritic arbor. We found that the spatial extents of dendritic arbors in the dLGN were smaller than those in the vLGN. We also explored related aspects of the circuitry and found that the dendritic arbors of cells in the dLGN were denser and more symmetrical than those in vLGN. All told, our results show that physiological differences between the dorsal and ventral LGN have structural correlates.

Receptive field size in the dorsal vs ventral division of the LGN.

Qualitative descriptions of receptive fields in the cat (Spear et al., 1977) and rat (Sumitomo et al., 1979) suggested that receptive fields in the vLGN were larger than those in the dLGN and usually lacked the center surround receptive field structure that many relay cells inherit from retina. We quantified these aspects of receptive field structure, in mouse. Our results show that, indeed, receptive fields in the vLGN are very large, ~25°-60° across. By contrast the largest receptive fields recorded from the dLGN were approximately 17°, at their widest point. Also, receptive fields in the vLGN were On, Off, or On-Off; none had a center-surround structure (Ciftcioglu, et al., 2014).

Correlation between size of the dendritic arbor and size of the receptive field.

The disparity in receptive field size between the subnuclei might result from differing amounts of retino-thalamic convergence. High convergence can result from two different wiring schemes. First, the axonal arbors of ganglion cells could span large distances to reach compact dendritic arbors. Alternatively, the dendritic arbors of thalamic cells could extend to retinal afferents that arborize at distant loci (Chklovskii et al., 2002). The first scenario can be excluded because axonal arbors of retinal ganglion cells that project to both divisions of the thalamus are spatially restricted (Hong et al., 2014). Thus, in principle, if the size of the dendritic arbor of a postsynaptic cell is small, then the receptive field of that cell will most likely be small and vice versa.

Accordingly, our morphological reconstructions of cells in the LGN support the idea that the basis of these large receptive fields is expansive dendritic arbors (Ciftcioglu et al., 2014). The results of Sholl analyses showed that the dendritic arbors of cells in the dLGN were compact; the average distance of intersection (of dendritic branches and Sholl circles) was 58 μ m. Variation among relay cells was small. On the other hand, the average distance of dendritic intersection for the vLGN was long, 155 μ m. There was considerable variation in branching patterns across the population as well. Moreover, the dendritic arbors of cells in the vLGN often spanned at least one axis of the entire subnucleus, sometimes even reaching into the dLGN and other adjacent structures.

Anisotropisms of the dendritic arbor in the vLGN

We asked if neurons in the vLGN sampled all regions of the nucleus equally or if there were a bias in the shape of the dendritic arbor. For this purpose we devised an index to measure isotropism of the cells in our dataset. The geometric mean of the index scores for cells in the vLGN was approximately fourfold smaller than for cells in the dLGN. Thus dendritic arbors in the vLGN have specific and strong spatial orientations. We have not, however, been able to correlate the axis of the dendritic arbor with response property. Also, little is known about the

spatial distribution of inputs to the vLGN. Thus the functional importance of the anisotropy is, as yet, unclear.

Relationships between synaptic physiology and the extent of the dendritic arbor

The intracellular signals we record from neurons in the two divisions of the LGN are quantitatively distinct (Figure xx). Our group previously showed that recordings from relay cells in the dLGN are dominated by large, retinothalamic EPSPs. By contrast, synaptic currents recorded from cells in the vLGN were typically small and it was often difficult to resolve individual events. This difference might reflect more than one factor. One cause might be related to the principle of synaptic scaling, which holds that the more inputs a neuron receives, the smaller the size of any individual input. We know that relay cells in the dLGN receive only few retinal afferents (Chen and Regehr, 2000) whereas our results show that cells in the vLGN are positioned to pool many inputs. A second contributing factor might result from the cable properties of the postsynaptic cell. A synaptic potential that originates at an electronically remote site on the dendrite would attenuate as it traveled to the soma and thus appear smoother and smaller than at the origin. The dendrites of cells in the vLGN are long and tapered, so one might predict that remote inputs attenuate before reaching the soma. By contrast, retinal inputs to relay cells in the dLGN arrive at electronically proximal sites (Hamos et al., 1987). Taken together, our physiological and anatomical results are consistent with each other and point to higher convergence values in the vLGN than the dLGN.

Functional Implications

Why do cells in the vLGN have such large receptive fields and commensurately expansive dendritic arbors? Connections of vLGN might provide a clue. Unlike relay cells in the dLGN, the vLGN does not project to cortex. Rather, it projects to many subcortical structures involved with guiding movement (Graybiel, A.M., 1974, Mackay-Sim, A et al., 1983, Berman, N., 1977). Some of these structures, the superior colliculus, in particular, receive retinal input themselves; further, many retino-recipient cells in the colliculus have small receptive fields. Thus it is possible that inputs from the vLGN convey information from large regions of visual space and help to coordinate or modulate the activity of groups of cells in downstream targets.

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