Response Selectivity Is Correlated to Dendritic Structure in Parvalbumin-Expressing Inhibitory Neurons in Visual Cortex

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Response Selectivity Is Correlated to Dendritic Structure in Parvalbumin-Expressing Inhibitory Neurons in Visual Cortex

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Inhibitory neurons have been shown to perform a variety of functions within brain circuits, including shaping response functions in target cells. Still, how the properties of specific inhibitory neuron classes relate to their local circuits remains unclear. To better understand the distribution and origins of orientation selectivity in inhibitory neurons expressing the calcium binding protein parvalbumin (PV) in the mouse primary visual cortex, we labeled PV+ neurons with red fluorescent protein (RFP) and targeted them for cell-attached electrophysiological recordings. PV+ neurons could be broadly tuned or sharply tuned for orientation but tended to be more broadly tuned than unlabeled neurons on average. The dendritic morphology of PV+ cells, revealed by intracellular labeling, was strongly correlated with tuning: highly tuned PV+ neurons had shorter dendrites that branched nearer to the soma and had smaller dendritic fields overall, whereas broadly tuned PV+ neurons had longer dendrites that branched farther from the soma, producing larger dendritic fields. High-speed two-photon calcium imaging of visual responses showed that the orientation preferences of highly tuned PV+ neurons resembled the preferred orientations of neighboring cells. These results suggest that the diversity of the local neighborhood and the nature of dendritic sampling may both contribute to the response selectivity of PV+ neurons.

Introduction
Inhibition has diverse roles in cortical circuits (Pouille and Scanziani, 2001; Wehr and Zador, 2003; Mariño et al., 2005; Cardin et al., 2009; Adesnik et al., 2012; Atallah et al., 2012; Lee et al., 2012; Lovett-Barron et al., 2012; Royer et al., 2012; Wilson et al., 2012). This diversity of function matches the diversity of the inhibitory population. Inhibitory neuron subclasses differ in their gene expression, axonal projection patterns, dendritic morphology, and electrophysiological properties, suggesting that specific subtypes may perform specific functions (Markram et al., 2004; Somogyi and Klausberger, 2005; Burkhalter, 2008; Isaacson and Scanziani, 2011).

Parvalbumin-positive (PV+) cells, often considered one distinct cell type, are heterogeneous across all of these dimensions. Morphologically, they include soma-targeting basket cells with small and large dendritic and axonal fields, axon-targeting chan-
We recorded from a large number of PV− neurons and found that highly tuned PV+ neurons have smaller dendritic fields and shorter dendrites, whereas broadly tuned PV+ neurons have larger dendritic fields and longer, more tortuous dendrites. We then compared the spatial distribution of orientation preferences of the neurons surrounding PV+ neurons, finding that the orientation preferences of PV+ neurons resembled those of nearby cells, suggesting that these neurons may sample uniformly from local inputs, and the breadth of their dendritic arbors may influence their response selectivity by restricting the number and diversity of their inputs.

Materials and Methods

**Mice.** Experiments were performed in mice of either sex under protocols approved by Massachusetts Institute of Technology’s Animal Care and Use Committee and conformed to National Institutes of Health guidelines. Heterozygous PV-Cre knock-in driver mice, which express Cre in >90% of PV+ neurons, were backcrossed into a C57BL/6 line (Hippcheney et al., 2005) and used for the analysis of PV− and PV+ neurons. Thy1-GFP-S mice (Feng et al., 2000), in which a subset of superficial layer neurons are labeled, were also maintained on a C57BL/6 line and were used for the analysis of pyramidal neurons.

**Viral construct and injection.** Red fluorescent protein (RFP) was expressed in PV+ neurons in V1 of PV-Cre mice by injection of an LS1L-RFP construct packaged into adeno-associated virus (serotype 2/9) as described previously (Kuhlman and Huang, 2008; Runyan et al., 2010). Six-week-old PV-Cre mice were initially anesthetized with 4% isoflurane in oxygen and maintained on 2% isoflurane. The skull was thinned along the eHP laser, passed through a Deep-See module (Spectra Physics), where the laser was tuned to 920 nm, and functional imaging was done through a high performance objective lens (25× Olympus XPL N objective, NA = 1.05). z-stacks were collected tangentially, at 2 μm increments from the pial surface through the extent of the filled cell, at resolution of 0.4 μm/pixel, spanning 200–400 μm in x and y dimensions, using Fluoview300 confocal imaging software (Olympus), on both the red (RFP+) and green (Alexa-488 dye) channels. In all filled cells, the signal on red and green channels overlapped throughout all processes, and photomultiplier tube gain was optimized to visualize the finest processes.

**Two-photon calcium imaging.** For these experiments, we used a Prairie Ultima two-photon system (Prairie Technologies) driven by Spectra Physics Mai-Tai eHP laser, passed through a Deep-See module (Spectra Physics). The excitation laser was tuned to 920 nm, and functional imaging was done through a high performance objective lens (25× Olympus XL Plan N objective, NA = 1.05). A glass pipette filled with Oregon Green Bapta-1 AM (1.0 mM, Invitrogen) and AlexaFluor-594 (100 μM, Invitrogen) was visually guided into the brain and lowered to a depth between 100 and 200 μm below the surface, near the center of the viral injection site, and a small amount of dye was released using a picospritzer. The brain was then left undisturbed for at least 1 h before imaging.

**Data analysis:** visual responses. Analysis of all data was performed off-line with custom written MATLAB routines. Electrophysiological time traces were imported into MATLAB, smoothed with a Gaussian kernel, and spikes were identified by detection of events based on the derivative of the voltage traces. The spontaneous firing rate of each neuron was measured for 30 s preceding visual stimulation for each trial. A neuron was considered visually responsive if its firing rate at the preferred orientation was significantly higher than its spontaneous firing rate, determined with a t test. The spontaneous firing rate was subtracted from the response to each orientation, the mean firing rate across the entire 4 s stimulus interval. The response firing rates were then fit to a Gaussian function.

Fluorescence time traces were assigned to the appropriate cell location, to obtain a time trace sampled at 50 Hz. The response (ΔF/F) was calcu-
lateral for each time point by subtracting and then dividing the fluorescence value by the mean fluorescence of the surrounding 100 time points. The maximum ΔF/F during each grating presentation was taken as the visual response (Schummers et al., 2008; Runyan et al., 2010).

The orientation selectivity index (OSI) was calculated as the vector average of responses in the preferred direction (Schummers et al., 2002). Statistical comparisons were performed using the Wilcoxon test, two-tailed t test, and the Kolmogorov-Smirnoff test and yielded indistinguishable results. Values from two-tailed t tests are reported in Results.

In the population calcium imaging datasets, the spatial arrangement of orientation preferences was assessed by calculating the local orientation scatter, or the mean difference in the preferred orientations of each cell and neighboring cells within 60, 90, 120, or 240 μm. This mean difference was compared between RFP+ cells and their neighbors and RFP− cells and their neighbors. To test the validity of the difference between the orientation mapping around RFP+ and RFP− neurons, a bootstrap procedure with 10,000 samples was used to estimate the orientation mapping in the randomized configuration, where the orientation preferences were resampled among the cells’ spatial locations with replacement, and the local scatter around each cell was recalculated in each scrambled iteration (Dombeck et al., 2009).

Morphological reconstructions. Neurons were reconstructed from tangential z-stacks that were collected in vivo, as described above, using V3D semiautomatic tracing software (Peng et al., 2010). The multi-TIF 16-bit image stacks collected with the Fluoview software were converted to high-contrast 8-bit images within ImageJ software and then imported into V3D. The contrast of each image was enhanced to allow the tracing of each thin dendritic process. Both the red (RFP+) and green (Alexa-488) channels were used to follow all of the neuron’s major and minor branches, and dendritic tips were then exported to MATLAB, where custom written software was used for the Sholl analysis (Gutierrez and Davies, 2007). The number of Sholl crossings was assessed at 20 μm increments. For each neuron, the Sholl profile was fit to a Gaussian function, from which the peak number of crossings (amplitude) and distance of the peak from the soma (displacement) were extracted. The maximal dendritic extent was calculated as the distance from the soma to the most distal dendritic tip, and the dendritic field volume was calculated by computing the convex hull of the 3D dendritic tip coordinates. The polarity of the dendritic branching was assessed as follows. The direction of each branch and tip relative to the soma in each of the three cardinal planes was measured. In each plane, a Dendritic Polarity Index

Figure 1. Relating structure and function in PV+ neurons in vivo. A, The orientation selectivity of RFP+ neurons and RFP− neurons was characterized in the primary visual cortex of PV-Cre mice injected with a fixed-RFP viral construct. RFP+ neurons were targeted for recording under two-photon guidance, with a patch pipette containing green dye (Alexa-488). Each cell was then electroporated with the dye, and a z-stack was collected through the extent of the dendritic tree to enable morphological reconstruction. Scale bar, 20 μm. B, Spikes recorded from RFP+ neurons (red) and RFP− neurons (blue) were averaged and normalized by their maximum voltage. Spikes recorded from the RFP+ neurons showed the characteristic shape of fast-spiking PV+ neurons, including a strong afterhyperpolarization. C, The spike shapes of RFP+ neurons and RFP− neurons were distinguishable by the ratio of peak to valley amplitude and spike width. RFP+ neurons are color-coded by their OSI, demonstrating that spike shape in RFP+ neurons did not predict orientation selectivity (p > 0.3). D, The histogram of OSIs of RFP+ (red, shaded by OSI) and RFP− (blue) neurons reveals a wide range of orientation selectivity in both RFP+ and RFP− neurons, although RFP+ neurons tended to be more broadly tuned than RFP− neurons on average (p < 0.01). E, Twenty RFP+ neurons were reconstructed (see Materials and Methods), flattened through the z-plane (dorsal-ventral) for illustration purposes only, and color-coded by OSI as in C–D. All neurons are oriented similarly, as if in a tangential section. A, Anterior; P, posterior; M, medial; L, lateral; F, Three representative examples across the OSI range are shown, along with their orientation tuning curves. Error bars on tuning curves indicate SEM. Cell numbers indicate the cell IDs from Table 1. Scale bars: E, F, 20 μm. **p < 0.01.
(DPI) was then calculated by vector averaging the distances of the tips and branches around the soma.

RFP+ neurons from brains of PV-Cre mice were reconstructed in vitro for comparison with the in vivo reconstructions using the RFP label. The Alexa-488 dye in neurons imaged in vivo did not survive perfusion, and so the same cells were not imaged in vivo and in vitro. Coronal slices were collected at 100 µm thickness, mounted on slides, and coverslipped. z-stacks were collected at 1 µm optical slices at 4 µm per pixel on a Zeiss LSM 5 Pascal Exciter confocal microscope with the 543 laser line (RFP+ fluorophore), and neurons were reconstructed as above.

**Results**

**Electrophysiological properties of PV+ neurons**

We expressed RFP in PV+ inhibitory interneurons in heterozygous PV-Cre knock-in mice (Kuhlman and Huang, 2008; Runyan et al., 2010) and used two-photon targeted cell-attached recording (Fig. 1A) to characterize 80 visually responsive RFP+ neurons and 49 visually responsive RFP− neurons in V1 of 32 PV-Cre mice. The spike shapes of the RFP+ and RFP− neurons were distinguishable (Fig. 1B,C): the RFP+ neurons had narrower...
spike widths (mean ± SD: RFP⁺, 2.9 ± 0.4 ms; RFP⁻, 3.1 ± 0.2 ms; p < 0.01, two-tailed two-sample t test here and below), and similar peak/valley amplitudes (RFP⁺, 6.7 ± 15.5; RFP⁻, 10.4 ± 16.5; p = 0.37) and repolarization rates (RFP⁺, 3.1 ± 2.3 V/s; RFP⁻, 2.8 ± 1.8 V/s, p = 0.61). The spontaneous firing rate was higher in the RFP⁺ neurons (RFP⁺, 1.2 ± 2.0 Hz; RFP⁻, 0.4 ± 0.7 Hz; p < 0.01), but the two populations had similar visually evoked firing rates (RFP⁺, 5.8 ± 5.9 Hz; RFP⁻, 5.3 ± 6.4 Hz; p = 0.67).

Tuning properties of PV⁺ neurons

The diverse response features of PV⁺ neurons have been previously described by us (Runyan et al., 2010) and others (Liu et al., 2009; Kerlin et al., 2010; Hofer et al., 2011; Zariwala et al., 2011). We aimed in this study to carefully evaluate the orientation selectivity of a large population of these neurons and to compare their morphological features to their response selectivity. For each neuron, we measured the response to 18 drifting gratings in 20-degree increments and calculated an OSI by vector averaging the response; the OSI can range from 0 (unselective for orientation) to 1 (responsive to only one orientation). On average, the OSIs were lower in the RFP⁺ population (RFP⁺, 0.46 ± 0.28, n = 80; RFP⁻, 0.61 ± 0.31, n = 49; p < 0.01), although both populations included very broadly tuned and very sharply tuned cells (Fig. 1D). All recorded RFP⁺ cells were located between 115 and 300 μm below the pial surface (mean depth, 173 ± 70 μm), and soma depth and orientation selectivity were not correlated (r = 0.18, p = 0.13). In addition, although not all RFP⁺ neurons showed the narrow-spike profile typical of fast-spiking PV⁺ neurons (Fig. 1C), none of the measured spike shape parameters correlated significantly with OSI (spike width, r = 0.15, p = 0.37; peak/valley, r = 0.07, p = 0.77; repolarization rate, r = −0.15, p = 0.54). Thus, it is unlikely that the highly selective PV⁺ neurons were a depth-based subclass, such as multipolar bursting cells, a subclass of regular-spiking PV⁺ neurons that is located primarily at the border between layers I and II (Blatow et al., 2003) (i.e., at typical depths of 90–100 μm).

Morphology of PV⁺ neurons: dendritic extent, but not complexity, correlates with orientation selectivity

Differing tuning strength may indicate the existence of functional subclasses of PV⁺ neurons that correspond to morphological subclasses, so we reconstructed the dendritic morphology of 20 RFP⁺ neurons for which we had also measured orientation selectivity (Fig. 1E). After each cell’s orientation tuning was characterized, it was filled with Alexa-488 (green) dye from the recording pipette, and a detailed z-stack in tangential view was collected through the extent of its dendritic tree on both the red and green channels with two-photon imaging.

The orientation selectivity of reconstructed RFP⁺ neurons represented the full range of broadly tuned and highly tuned OSIs we described in Figure 1D (0.09–0.87). Qualitative examination of the reconstructions suggested that the dendritic morphology of RFP⁺ neurons might vary systematically with orientation selectivity. The transition from larger dendritic trees to smaller dendritic trees as tuning becomes sharper is evident across the full population of reconstructed RFP⁺ neurons, ordered by increasing OSI (Fig. 1E) and in three representative neurons spanning the full range of tuning (Fig. 1F).

We first estimated the spatial extent of the dendritic trees by measuring four parameters for each reconstructed RFP⁺ neuron: (1) the total dendritic length of all of its dendritic processes, (2) the maximal dendritic extent (distance from the soma to the most distal dendritic tip), (3) the dendritic field volume (the convex volume enclosed by the dendritic tips), and (4) the distance of maximal dendritic branching from the soma (Sholl analysis). All four measures were significantly correlated with each other (p < 0.05, Spearman’s rank correlation coefficient, here and below unless otherwise stated) and with orientation selectivity (Fig. 2A: dendritic length, r = −0.49, p < 0.05; maximal dendritic extent, r = −0.57, p < 0.01; dendritic field volume, r = −0.48, p < 0.05; peak branching distance, r = −0.58, p < 0.01).

Next, we assessed dendritic complexity with two parameters: (1) the peak number of branches as a function of distance from the soma (Sholl analysis) and (2) the total number of dendritic segments. The two measures of dendritic complexity correlated with one another (r = 0.8, p < 0.001), but unlike the measures of dendritic extent, neither measure correlated significantly with orientation selectivity (Fig. 2B: peak Sholl branches: r = 0.17, p = 0.47; total number of segments: r = 0.17, p = 0.46). Finally, ranking each dendritic segment by the number of branches separating it from the soma, orientation selectivity did not signifi-
cantly correlate with the number of segments of low or high order (p > 0.1 for all ranks).

To assess whether the directionality of dendritic branching correlated with the orientation selectivity of RFP + neurons, the angles of dendritic branches and tips from the soma were calculated in each of the three 2D planes. The polarity in each dimension was quantified by vector averaging, to obtain a DPI. The maximum DPI was not correlated to orientation selectivity, as calculated in each of the three 2D planes. The polarity in each dimension of the Sholl parameters (peak number of crossings, distance of peak from the soma, profile radius, and maximal dendritic extent (μm)) correlated with the orientation selectivity of RFP + neurons significantly different between the cells imaged in vivo and in vitro.

### Orientation preference maps of PV + and PV − neurons

The correlation between sharper orientation selectivity of PV + neurons and smaller dendritic lengths and arbor extents suggested that PV + neurons might derive their tuning by sampling their cortical neighborhood, and sharper tuning may reflect focal sampling of locally homogeneous orientation representations. We thus examined the relationship between the tuning of PV + neurons and surrounding neurons in the local V1 orientation map. Specifically, we used targeted, high-speed, two-photon calcium imaging (Wilson et al., 2012, 2013) to measure the orientation preferences of visually responsive RFP /PV + neurons and their neighbors (Fig. 5A–C). Among imaged cells, 77 of 105 RFP /PV + neurons and 1393 of 1601 RFP − neurons in four mice were visually responsive.

The preferred orientations of cells and their neighbors across the field of view were then compared (Fig. 5A–C). We identified RFP + cells with a range of OSIs, including high and low OSIs (Fig. 5D). The local orientation scatter surrounding each cell was calculated by measuring the difference between that cell’s preferred orientation and those of the neighboring cells within 60, 90, 120, or 240 μm (Fig. 5E, pooling all RFP + and RFP − cells from 4 animals); these distances included the maximal dendritic extent for highly tuned cells (<150 μm), and the maximal dendritic extent of most broadly tuned cells (~250 μm; Fig. 2A). The orientation scatter surrounding both RFP + and RFP − neurons increased with distance, being significantly greater at 240 μm than at 60 or 90 μm (p < 0.05 comparing scatter of RFP + or RFP − neurons at 60 and 90 μm with 240 μm), reflecting the existence of local homogeneities in the orientation map that dissipate at larger distance scales.

However, the scatter surrounding RFP + neurons was significantly lower than the scatter surrounding RFP − neurons at all distance scales (60 μm, p < 0.01; 90 μm, p < 0.01; 120 μm, p < 0.01; 240 μm, p < 0.01); that is, RFP + neurons tended to have
Table 2. Response features and morphological measurements of reconstructed GFP-pyramidal neurons in Figure 4

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<th>Spontaneous firing rate (Hz)</th>
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<th>Total dendritic length (mm)</th>
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<th>Dendritic field volume (mm³)</th>
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Figure 4. Control dendritic reconstructions of pyramidal neurons in vivo, RFP⁻/PV⁺ neurons in vitro, and comparison with in vivo reconstructions of RFP⁻/PV⁺ neurons showing similar representations of full dendritic morphologies. A, For comparison, pyramidal neurons from the Thy1-GFPS mouse line were reconstructed. Reconstructions of three example pyramidal neurons are presented as in Figure 1E–F, with apical processes colored in yellow and basal processes in green. Scale bar, 20 µm. B, Dendritic morphology is similar in RFP⁻ neurons reconstructed in vivo and in vitro, and distinct from GFP⁺ pyramidal neurons. The Sholl profiles of the RFP⁻ PV⁺ neurons imaged in vitro (bold red) and GFP⁺ pyramidal neurons imaged in vivo are superimposed on the in vivo RFP⁻ data from Figure 2 (pink). The in vitro Sholl profiles overlap extensively with the in vivo RFP⁻ Sholl profiles. Peak number of crossings (p = 0.28), distance of the peak from the soma (p = 0.22), and radius (p = 0.39) of the Sholl profiles were statistically similar in the in vitro and in vivo imaged cells, and distinct from pyramidal neurons (p < 0.001). C, Histogram of the total dendritic length of GFP⁺ pyramidal neurons (green), RFP⁻ neurons imaged in vitro (red), and RFP⁺ neurons imaged in vivo (pink). The total dendritic length was statistically similar (p = 0.30) between the two sets of RFP⁻ cells; however, both groups of RFP⁻ neurons had shorter dendrites than the GFP⁺ pyramidal neurons (p < 0.001). The morphological similarity between reconstructions of RFP⁻ neurons in vivo and in vitro suggests that in vivo imaging fully captured the dendritic arbors of these neurons.
Figure 5. RFP+ neurons tend to share the orientation preferences of their neighbors. A–C, Left column, RFP+ neurons (red) and surrounding RFP- neurons were loaded with the calcium dye Oregon Green Bapta-1AM (green). Three representative networks are shown. The blue lines indicate the scan paths used to image calcium responses. White asterisks indicate the first and last pixels from which each cell’s fluorescence response was collected within the scan path. Scale bar, 10 μm. Middle column, Example fluorescent responses to the 18 episodically presented drifting gratings (18 directions; gray represents 4 s OFF; white represents 4 s ON), from cells in each of the example networks (blue represents RFP+ neuron responses; red represents RFP- neuron responses). Right column, Each neuron is color-coded by its preferred orientation, and RFP+ neurons are indicated by red halos. A, RFP+ OSIs: cell #2, 0.23; #15, 0.84; #27, 0.80; #32, 0.29; #66, 0.48. B, RFP- OSIs: cell #7, 0.92; #8, 0.6; #30, 0.32; #39, 0.59; #44, 0.38. C, RFP+ OSIs: cell #2, 0.74; #8, 0.31; #28, 0.51; #30, 0.35. D, The OSI spanned the full range from 0 (untuned) to 1 (highly tuned) in both RFP+ (red) and RFP- (blue) neurons, consistent with the electrophysiology measurements of Figure 1. E, The local scatter in orientation preference surrounding each neuron within expanding intercell distances (red represents RFP+ neurons; pink, RFP+ in same networks with scrambled orientation preferences; dark blue, RFP+ neurons; light blue, RFP- in same networks with scrambled orientation preferences). The scatter surrounding RFP+ neurons was significantly lower than the scatter surrounding RFP- neurons (p < 0.01), or RFP- neurons in scrambled networks (p < 0.01). Error bars indicate SEM. **p < 0.01.
visual cortex (V1), using two-photon targeted cell-attached recordings. Although PV\(^+\) neurons are less selective for orientation on average than the rest of the V1 neuronal population, the distribution of orientation selectivity in PV\(^+\) neurons includes highly tuned cells in addition to broadly tuned cells. This diversity of tuning correlates with dendritic morphology: highly tuned PV\(^+\) neurons have shorter total dendritic lengths, maximal branching closer to the soma, smaller dendritic field volumes, and shorter maximal dendritic extents compared with broadly tuned PV\(^+\) neurons. Dendritic branching complexity, however, shows no relation to tuning. Furthermore, the orientation selectivity of PV\(^+\) neurons is more similar to that of their local neighbors compared with non-PV\(^+\) neurons. Thus, the tuning of PV\(^+\) neurons may derive from sampling of local inputs coupled with their dendritic morphology: highly tuned neurons, for example, may derive their tuning by sparsely sampling a homogeneous local population with short, proximally branched, dendrites, whereas broadly tuned neurons may derive their tuning by extensively sampling a more heterogeneous population with longer, distally branched dendrites.

Several studies have now examined the orientation selectivity of inhibitory neurons in the mouse visual cortex; we and others have described the existence of both highly tuned and broadly tuned inhibitory neurons (Niell and Stryker, 2008; Ma et al., 2010; Runyan et al., 2010; Zarivala et al., 2011), whereas others have described only broadly tuned inhibitory neurons (Sohya et al., 2007; Liu et al., 2009; Kerlin et al., 2010). In the present study, we sampled a large number of PV\(^+\) inhibitory interneurons (\(n = 80\) visually responsive PV\(^+\) neurons) to describe the distribution of orientation selectivity in this population more reliably, finding an overall more broadly tuned distribution than the rest of the V1 population, but a significant number of sharply tuned neurons as well. Differences in targeting and recording methods could account for the smaller, highly tuned, subclass missing from some studies (Hasenstaub and Callaway, 2010), as each study has used a unique combination of transgenic mice and recording techniques (Liu et al., 2009; Kerlin et al., 2010; Ma et al., 2010).

The existence of functionally diverse PV\(^+\) neurons implies that these neurons may derive their inputs in different ways. The dendritic trees of PV\(^+\) neurons were carefully and completely reconstructed in this study (Fig. 1). Fine-resolution z-stacks captured the full dorsal-ventral extent of the dendritic trees, whereas post hoc image processing to enhance the image contrast and careful manual tracing allowed each fine dendritic process to be traced through its full extent. PV\(^+\) neurons imaged in slices and reconstructed with identical methodology yielded highly similar (Dra¨ger, 1975; Kerlin et al., 2010). Local coherence in the orientation selectivity of PV\(^+\) neurons is more similar to that of their local neighbors compared with non-PV\(^+\) neurons. Therefore, the tuning of PV\(^+\) neurons may derive from sampling of local inputs coupled with their dendritic morphology; highly tuned neurons, for example, may derive their tuning by sparsely sampling a homogeneous local population with short, proximally branched, dendrites, whereas broadly tuned neurons may derive their tuning by extensively sampling a more heterogeneous population with longer, distally branched dendrites.

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The finding that the orientation selectivity of PV\(^+\) neurons is correlated with the orientation distribution of cells in their local neighborhood is in agreement with recent work suggesting that inhibitory neurons receive strong local inputs from nearby cells (Bock et al., 2011; Hofer et al., 2011). Because V1 in rodents lacks the highly ordered orientation maps found in carnivores, it has been commonly assumed that orientation preferences are uniformly random across the rodent visual cortex (Ohki and Reid, 2007). However, our results in mouse V1 confirm longstanding hints that local clustering of orientation preferences exists (Dräger, 1975; Kerlin et al., 2010). Local coherence in the orientation map, combined with sparse and highly local sampling of inputs by some inhibitory neurons, could lead to high selectivity in these cells. Future studies examining the outputs of highly tuned and broadly tuned inhibitory neurons will determine whether these neurons also select their targets according to such spatial rules, or in functionally specific ways (Yoshimura and Callaway, 2005; Fino and Yuste, 2011; Packer and Yuste, 2011; Wilson et al., 2012).

References


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Reference


