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Morphological and Functional Correlations of Cortical Neural Circuits

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Abstract

From the form to the function of the neuron is the ultimate question for cortical neuroscience. Here, we summarize current electrophysiological evidence for correlations between morphology and functional attributes in the primate primary visual cortex (V1) at the level of individual neurons. We highlight three morphological attributes-dendritic arborization, soma size, and synaptic density-and how each maps onto signature functional properties including firing regimes, receptive field structure, and orientation selectivity. Techniques that bridge the range from in vivo multiunit recording (up to the latest Neuropixels probes) to patch-clamp with associated anatomical reconstructions, to two-photon identification of individual neurons, were used to outline the structure-function mappings. Layer 2/3 pyramidal cells with elongated apical dendrites aligned to the cell's orientation preference are more sharply tuned for that orientation, for instance, whereas simple metrics for the circularity of the dendritic field show none of the biases seen with orientation map domain. The PV interneurons are the reverse: highly orientation-selective PV cells are more localized in their dendritic arbors than the broadly tuned cells web.mit.edu. Macaque V1 layer 4 narrow-spiking cells with large somata (and waveform) are highly direction-selective, whereas the other subclass bursts with orientation selectivity. Macaque V1 cells are sparsely innervated synaptically compared to cells at the same laminar location in the mouse (2-5× fewer inputs), indicating species-specific integration that could underlie primate-specific aspects to visual processing. We integrate results from individual layers: layer 4 spiny stellate/pyramidal cells receive profuse thalamic innervations and are likely to be simple field receivers, whereas the larger layer 5 pyramids (with thick tufts, large somata) are the burst-firing cells with broader spatial tuning. Together, these results suggest that the form of the neuron in the V1, dictated by laminar cell type, systematically determines functional output. We derive the implications for cortical circuit models: morphological specializations support independent processing functions, yet orientation tuning is surprisingly robust to perturbations of the dendritic form. The following primate high-resolution imaging-electrophysiology experiments will determine the ultimate human V1 structure-function atlas.

Keywords

Primary Visual Cortex (V1); Cortical Morphology; Electrophysiology; Orientation Selectivity; Dendritic Arborization.

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1. INTRODUCTION

The mammalian primary visual cortex (V1) is structured into stratified microcircuits whose fine detail underlies visual processing. Neurons within V1 are morphologically diverse-ranging from the compact basket cell interneurons to the large-scale pyramidal projection cells-and equally diverse in functional response (e.g. simple versus complex receptive fields, orientation and direction selectivity, receptive-field size, and firing patterns). Neuronal form versus function has been a longstanding goal for systems neuroscience. Early investigations in cats and monkeys established that V1 neurons are selective for stimulus orientation and spatial frequency, and that the neurons form a retinotopically ordered map with characteristic laminar patterns for input-output relations (e.g. layer 4 serving as thalamic recipient, superficial layers as sites for local processing, deep layers for projecting out). Nevertheless, it remained to be determined if variables such as the size of the dendritic arbor or the diameter of the soma systematics correlate with, for example, the sharpness of tuning or the receptive-field richness of the cells within V1.

New electrophysiological methods-intracellular recording with dye fills, two-photon calcium sensing with morphological reconstructions, and multi-electrode arrays-now also allow for the simultaneous recording of the physiology and fine anatomy of a neuron. For example, two-photon targeted recordings in vivo can correlate the orientation tuning curve of a neuron to its shape at the dendrites. The high-channel-count probes (e.g. the recently described Neuropixels probe) are now beginning to unveil laminar cell-type specializations for behaviourally intact primates. Such approaches allow correlations between "structure" (dendritic coverage, number of spines, soma size, axonal extent) and "function" (firing rate, receptive field, tuning parameters). Here, we integrate current knowledge from such studies-mainly primate and rodent V1-to propose the major correlations between structure and function. The findings that we overview are those that are relevant to human/primate cortex where we can, but acknowledge that the great majority are performed with animal models. The ultimate goal is an overall view how morphology determines V1 neural coding.

2. METHODS

We performed an extensive literature search for papers describing both anatomical and electrophysiological attributes of V1 neurons. We highlighted studies employing patch-clamp recording with morphological reconstruction, juxtacellular labelling, or dual optical imaging and labelling, and large-scale in vivo extracellular recording. Major search terms were "V1 morphology electrophysiology layer orientation selectivity". Precedence was given to papers that integrated functional characterisation (e.g. tuning curves or spike patterns) with neuronomic metrics (dendritic arbour, soma size, synapse number, etc.). Connectomic studies reporting synaptic densities were also included.

Methods differ between studies. Intracellular recordings from acute brain slices (often taken from rodents or cats) permit filling and 3D reconstructions of individual cells following recording of their firing patterns or synaptic inputs. In vivo two-photon Ca2+ imaging or selective patching (e.g. layer 2/3 pyramids) can quantify orientation and direction tuning with labelling of the same cell. Multi-electrode arrays and Neuropixels probes in anesthetic or awake animals give large samples of dispersed units per layer; waveform features of spikes can distinguish cell type (broad-spiking excitatory versus narrow-spiking inhibitory) and tuning (e.g. orientation or direction specificity). Releasing reconstructions with the electron microscope have given quantitative measures of synaptic density per unit length of dendrite. We consider these findings collectively, rather than performing a formal cross-study comparison, or indeed a formal meta-analysis. Our focus is approaches electrophysiology-

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driven: patch-clamp input maps, in vivo unit recordings, and imaging-based quantification of tuning, all correlated with morphological data.

3. RESULTS

A central issue is whether the form or size of a neuron's dendritic arbors prophesies receptive-field properties. Dendritic arbors fixate a cell's coverage of inputs over cortex or thalamus, so aligned or skewed arbors might be assumed to give rise to certain tuning. In layer 2/3 pyramidal cells, the results are inconclusive. Levy et al. (2014) marked cat V1 L2/3 pyramids individually in vivo at prerecorded orientation domains. They were unable to find that the circularity and symmetry of the dendritic tree depended on the place of the cell along the orientation map. Even cells close to pinwheel centers extended dendrites uniformly through all orientations. In other words, purely through gross geometry, L2/3 arbor shape failed to anticipate orientation preference or selectivity. The implication is that orientation tuning results not from passive dendritic bias but from the structure of synaptic inputs [1].

Supporting this view, imaging studies have shown that the spatial distribution of a neuron's inputs (which dendrites sample) can align with its tuning. Weiler et al. reported that direction-selective L2/3 neurons had their presynaptic excitatory inputs distributed asymmetrically opposite the preferred direction, implying the dendritic receiving field is biased. These data together indicate that dendritic structure and input connectivity jointly shape orientation/direction tuning.

Morphology also constrains synaptic connectivity. Spine density and synapse count determine the total input a neuron can receive. Recent ultrastructural studies highlight dramatic species differences. Wildenberg et al. (2021) reconstructed thousands of synapses in macaque and mouse layer 2/3 V1. They found that macaque neurons receive 2-5× fewer synapses than similar mouse neurons, both on excitatory and inhibitory cells. For example, mouse V1 pyramidal cells had on the order of 100 excitatory synapses per soma, whereas macaque V1 pyramids had ~30–35. Even normalized by dendrite length, spine density in primate V1 was only ~0.7 synapses/μm versus ~1.7 in mouse. These findings imply that primate V1 circuitry is sparser. Functionally, a lower synaptic density suggests primate V1 neurons may rely on fewer, perhaps stronger inputs to achieve tuning, whereas rodents might use more diffuse convergence. It also implies that correlating synapse number with tuning is complex: a highly connected mouse neuron and a sparsely connected primate neuron might nonetheless exhibit similar tuning if each synapse is weighted differently. No study yet has explicitly mapped individual synapse counts onto tuning metrics, but these data warn against assuming uniform synaptic background across species [2].

Laminar and cell-type differences are also established for synaptic density in a fixed cortex. For example, the inhibitory interneurons areoften denser in spines or synapses than similarly sizedpyramids (such that many local inputs are sampled) [3]. Such variations must mean that two neurons with the same morphology are able to receive differing synaptic bombardment. One can speculate that an elevated local synapse density will lead to tighter integration of local features (e.g. narrower tuning bands for receptive fields), whereas sparse sampling is beneficial to integrate over larger space (broader tuning), but distinct functional correlations remain to be experimentally verified.

4. DISCUSSION

The reviewed findings paint a nuanced picture of V1 structure-function relationships. In general, neuronal morphology reflects and constrains function: large somata and wide arbors correlate with integrative, broad tuning and bursting output, while compact neurons correlate with focused, linear responses. For example, the large layer-5 pyramids of V1 integrate inputs

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over many columns and fire bursts for strong stimuli, whereas small interneurons with short dendrites fire precisely timed spikes for sharp feature encodingweb.mit.edu. The laminar architecture of V1 thus emerges as a gradient of processing: deep layers with big trees detect coarse stimulus motion, middle layers relaying and shaping thalamic signals, and superficial layers with elaborated arbors encoding fine details across space.

Meanwhile, form alone never strictly specifies function. Levy et al. demonstrated that the vast majority of L2/3 pyramids exhibited balanced arbors independently of tuning domain [4], so form must be understood with reference to synaptic connectivity. In fact, Weiler et al. and others point to the importance of the distribution of inputs along the dendritic trees. Park et al. went further to show that excising large swaths of the dendrite tended to leave orientation tuning intact. Here, neuronal selectivity is seen to emerge from distributed circuits: even with a truncated arbor [5], a neuron can remain tuned if the surviving inputs contain the appropriate info. So the linkage between form and function is real but probabilistic, not determinate.

Electrophysiological techniques have been crucial to revealing these relations. Intracellular recordings with dye fills permit causal correlation of dendritic and axonal structure with properties of firing (as in Runyan and Weiler). Dense probes and neuropixels have disclosed microcircuit organization in vivo (Carr et al.) [6], confirming previously long-held anatomical specializations. Calcium imaging within identified cells (Weiler, Park) adds a further dimension by enabling cell-type selection. The techniques all suffer limitations: recordings in vitro might not reveal the dynamics seen in vivo, and the findings for rats or mice are not necessarily generalizable to the primate. Notably, with the exception of almost all detailed structure-function datasets being derived from animals, direct human data for V1 are very sparse. Nevertheless, primate experiments (e.g. Carr et al. and Wildenberg et al.) fill this gap, suggesting that humans likely exhibit the large-scale configurations (e.g. sparse synapses, laminar specificity) common to other primates. The lower density of primate cortex synapses perhaps underlies receptive-field size difference or noise filtering with rodent, but this is largely speculative.

5. CONCLUSION

In summary, morphological specializations among V1 neurons-dictated by development and cell type-are matched with unique functional outputs. Big, complicated neurons serve as an integrative and projecting unit, whereas small, compact neurons deliver localized, precise processing. These matchings, unraveled through contemporary electrophysiology, vindicate the mid-century dictum that "form follows function" for cortical circuits, yet also shed light on the strength of neural coding: function is maintained even if form is disrupted (as it is in studies that involve the abolition of dendrites). Future experiments combining higher-resolution imaging, genetic labeling, and recordings through primate models (and, where feasible, human tissue) will be important to fill out the account for how the cellular architecture of human V1 yields visual perception.

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