

Building maps from maps in primary visual cortex

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Neurons in the visual system respond to more complex and holistic features at each new stage of processing. Often, these features are organized into continuous maps. **Could there be a fundamental link between continuous maps and functional hierarchies?** Here, we review recent studies regarding V1 maps providing some of the most noteworthy advances in our understanding of **how and why maps exist**. In particular, we focus on the common theme that some maps are inherited from the input of parallel pathways, which are then intimately linked to the emergence of new functional properties and their corresponding maps. **These results on V1 maps may prove to be a unifying framework for hierarchical representations in the visual cortex.**

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Introduction

Primary visual cortex (V1) has been a model system in the study of cortical computation largely because of the detailed methods available to characterize its inputs and outputs. The parallel inputs from the lateral geniculate nucleus (LGN) [1] undergo salient transformations within the V1 circuit that have been rigorously quantified. **In the effort to determine wiring rules that govern cortical transformations**, we may find clues in the spatial relationships between functional maps arising at successive processing stages in V1. In this respect, an important characteristic of thalamocortical architecture is the **recapitulation of the LGN laminar segregation across the horizontal dimension of V1**. Ocular dominance columns are the most classic example of this architecture. Other examples include the WXY channels in the cat, and parvocellular, magnocellular and koniocellular (PMK) channels in the monkey, which make patchy projections across the cortical surface [1,2]. Lastly, pathways segregated by On/Off responses have been shown to provide clustered inputs to layer 4 of carnivores [3–5]. Recent experiments show that this

afferent clustering may be important for establishing new response properties. The new data support a scheme **linking functional V1 maps inherited from the LGN to maps of tuning properties that emerge in V1**. Here, we focus on four recent areas of study that support this scheme: firstly, the emergence of disparity tuning maps from ocular dominance in the cat; secondly, the inheritance of spatial frequency maps from PMK pathways in the primate; thirdly, the emergence of orientation maps from On/Off pathways in the cat; and finally, the development of direction maps from orientation maps in the ferret. **These new studies suggest a general motif of cortical processing whereby the spatial structure of cortical maps is a crucial substrate for establishing new response properties.**

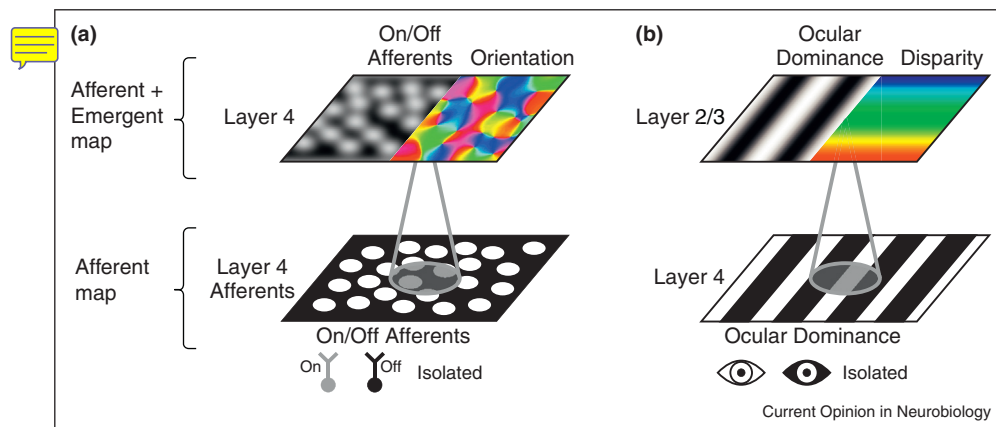
Left-right eye pathways

→ ocular dominance maps

→ disparity maps

In layer 4 of V1, signals from the two eyes are well segregated such that most neurons only respond to one eye [6,7]. These pathways finally converge in the superficial layers of V1 while still maintaining a significant degree of preference for one eye over another (Figure 1). Not coincidentally, tuning for the disparity of input between the two eyes also arises in the superficial layers. Given the clear dependence of disparity on binocular integration, electrode studies showing that these two features are largely uncorrelated across a population of V1 neurons [8,9] once seemed counterintuitive. Recent two-photon imaging experiments in the cat now help to reconcile this issue [10•]. The two-photon experiments demonstrated that there are maps for phase disparity, which run orthogonal to the ocular dominance maps. This orthogonality is consistent with the previously shown independence on a cell-by-cell basis [8,9], yet it constrains hypotheses attempting to explain how the circuit is wired to create disparity from binocular integration. Furthermore, the **disparity maps** suggest an additional factor that might be at play — the putative spatial phase maps in layer 4 [11–13,14•] created from clustering of On and Off geniculate afferents [3–5]. More specifically, maps of binocular phase disparity could be established by integrating phase maps from each eye. An interference pattern of spatial phase between the two eyes would run along the transition zones of the ocular dominance map, consistent with the observed orthogonality between maps of disparity and ocular dominance. Importantly, any model explaining the generation of disparity maps also has to account for the orthogonality between orientation and ocular dominance [15–17], along with the relationship between orientation preference and the clustered On/Off geniculate afferents [18•] discussed below.

Figure 1



Two examples of the hierarchy of afferent and emergent maps. Through convergence, functional segregation at one level in the processing hierarchy gives rise to an afferent and an emergent map at the next level. (a) On-center and Off-center LGN afferents are clustered in layer 4. They converge within layer 4 (afferent map), where they serve as the seed for the orientation map (emergent map). (b) Layer 4 is divided into bands of ocular dominance — regions of cortex that respond to stimulation of one eye over the other. The signals from both eyes converge in layer 2/3, where a preference for stimulation of one eye over the other still exists (afferent map). This convergence in information from both eyes may be the seed for the disparity map found in layer 2/3 (emergent map).

PMK pathways → spatial frequency maps

Another important set of channels that have been thought to yield V1 maps are the PMK pathways in the primate and the WXY channels in carnivores. This class of pathways captures unique bands of spatial, temporal, and chromatic information. In the cat, maps have been proposed based on these channels [19]. Here, we focus on the primate PMK pathways in light of their relevance to recent work showing spatial frequency organization in monkey V1 with two-photon imaging [20^{••}]. The PMK pathways all make their way to layer 2/3 via local V1 circuits, as well as directly from the LGN. In general, the cytochrome oxidase blobs, which coincide with the center of ocular dominance columns, are linked to the pathways' clustering across the 2/3 surface. The P pathway, with its smaller receptive fields, targets both blobs and interblobs equally. Both M and K pathways, which have larger receptive fields, terminate predominantly in the blobs, although with a lesser degree of segregation for the M than the K pathway [21,22]. Consistently, electrode studies have shown that blobs in the monkey tend to have cells with lower spatial frequency preference [23,24].

Recently, it was shown with two-photon imaging that there are continuous maps of spatial frequency tuning in layer 2/3 [20^{••}]. The orthogonality between the orientation and spatial frequency maps is consistent with a spatial coincidence between blobs and low spatial frequency regions: blobs lie at the center of ocular dominance bands, and ocular dominance bands are orthogonal to orientation maps [15,25]. An alternative to the hypothesis that the observed spatial frequency maps arise from clustering of the PMK inputs to layer 2/3 is that they

originate from the On/Off clustering shown in layer 4 in carnivores [3–5]. As discussed in more detail later, a periodic interference between the On and Off retinal mosaic has been proposed as the underlying cause of the orientation map [14^{••}]. Such interference could also create a 'beat' in spatial frequency — regions of more overlap between On/Off afferents (higher spatial frequency) would gradually transition to regions of less overlap (lower spatial frequency). In general, it is important to consider that preferred spatial frequencies differ by four octaves across adjacent extremes of the map [20^{••}]. It seems difficult for such a large bandwidth to be accounted for through inheritance of the P, M, or K pathway alone.

On/Off pathways

→ On/Off maps

→ orientation maps

Hubel and Wiesel's simple model to explain the generation of orientation [26] tuning from LGN input has been repeatedly scrutinized ever since it was introduced [27]. However, the general notion that the feedforward footprint of circularly symmetric LGN receptive fields establishes orientation tuning has persisted. A recent study on this topic has produced some of the most revealing evidence regarding the generation of orientation tuning to date [18^{••}]. Building directly on prior work demonstrating clustering of On-center and Off-center afferents in layer 4 of the cat [5], the new study now shows that the ensemble of LGN afferents impinging on a V1 column predicts the V1 orientation preference. Unlike the Hubel and Wiesel model that employs strict alignment in the thalamocortical wiring to generate orientation tuning, the new data suggest that the tuning is instead 'seeded' via

inherited biases in **On/Off clustering**. Importantly, **the substantial overlap in On/Off receptive fields observed in [18**]** means that additional mechanisms must be at work to strengthen V1 tuning, such as cortical inhibition [28] and/or thalamic synchrony [29].

How is the On/Off clustering in layer 4 established? Motivated by an explanation for how orientation maps are built, previous studies have proposed answers [11,12,30,31]. **A model proposed by Miller accounts for On/Off clustering based on Hebbian learning rules that create competition between the On/Off afferents.** A similar idea was also proposed by Nakagama *et al.* [12]. Miller's model has been broadly applied to account for other forms of inherited maps, such as ocular dominance [32]. However, see [33] for a critique on inconsistencies with measured maps. **A different model, developed by Paik and Ringach, proposes that On/Off clustering in V1 is a reflection of the retinal ganglion cell mosaic [14**,30].** **With sufficient sparseness in sampling by the retina there will be local biases in On or Off input at each point in the visual field.** This last model predicts some previously unknown properties of orientation maps. First off, the interference pattern between the On/Off mosaics produces a periodic orientation map that has a hexagonal autocorrelation function, which is consistent across multiple species [14**] (but see also [34]). Second, the model predicts a correspondence between the rotational alignment between pinwheels and the global axis of the retinotopic map [31]. All the aforementioned models predict spatial phase continuity within the cortex [13]. However, **they differ in how the orientation maps are related to local retinotopic distortions.** Such commonalities and differences should be testable with two-photon imaging and electrode arrays. Furthermore, it will be interesting to see if they are consistent with the seemingly universal property of pinwheel density within spatial periods of the map [35*].

Orientation maps → direction maps

Functional maps emerging in V1 also seem to give rise to additional functional maps within V1. One example of such a 'second order' map is the direction map found in V1 in the cat and ferret [36–39]. Both the relative alignment and developmental time courses suggest that the orientation map seeds the direction map. The direction map is nested in the orientation map: Iso-orientation domains are often split into two iso-direction domains preferring opposite directions of motions. This organization suggests that the direction map is optimized with respect to coverage and continuity, but only within the limits set by the orientation map. The developmental time courses of orientation and direction maps provide additional evidence supporting the notion that the orientation map seeds the direction map. A series of studies in the ferret have demonstrated that while orientation maps are already present at eye opening,

the direction map develops after eye opening, and critically depends on visual experience during a precise time window [40,41**].

While there is strong evidence for direction maps in V1 of cats and ferrets, the same is not the case in the monkey [42,43]. **Unlike cats and ferrets [36], direction selective cells in monkey V1 are found in only a subset of layers [44,45].** It is quite possible that the lack of columnar organization results in a less continuous map, both factors making it difficult to detect using optical imaging. An analogous situation may be true for spatial frequency maps in the monkey, which required the resolution of two-photon microscopy for robust detection [20**]. Direction selective maps do indeed exist in the thick/pale stripes of macaque V2 [43] and MT [46]. V2 thick stripes and MT receive direct input from direction selective cells in V1 layer 4B [1], but **it remains to be seen how V1 precisely contributes to the direction maps in MT and V2.**

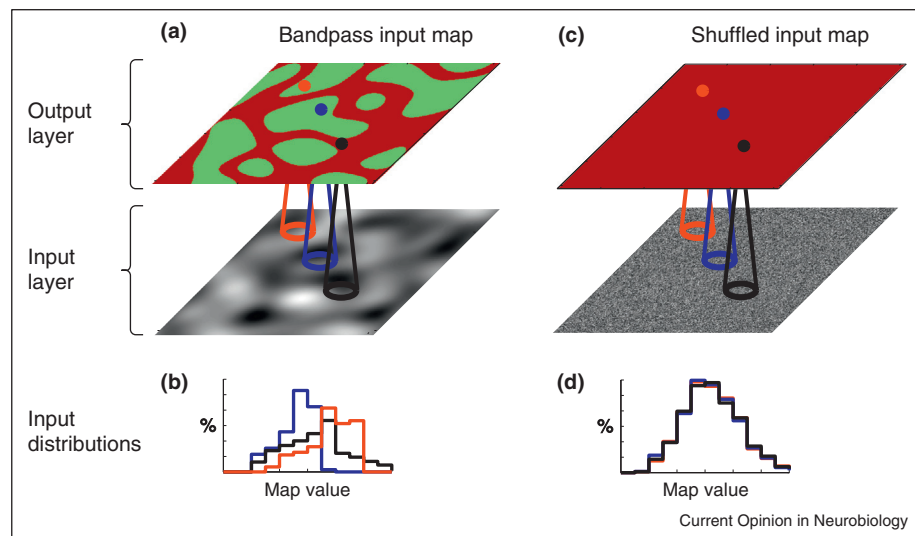
Concluding remarks

Function from map structure

Why does the cortex have continuous functional maps? Perhaps the cortex needs neurons with similar tuning at each processing stage to be wired together, in which case **spatial continuity of function minimizes wiring length [47].** **In addition, continuous maps may be necessary for downstream stages to systematically compute new features [48,49].** For instance, **two orthogonally aligned feature maps would allow for downstream areas to more easily compute the existence of all possible permutations of the two features.** Assume that neurons in V2 need to compute the coincidence of multiple spatial frequencies at a single orientation (e.g., for sharp edge detection) from their V1 input. **It was shown that a consequence of the orthogonality between orientation and spatial frequency is an anticorrelation between their local diversity [20**]** — a V1 region with consistent orientation preference (i.e. an 'iso-domain') contains diverse spatial frequency preferences, and vice versa. Thus, given other constraints on spatial phase, sharp edge detection would be feasible using an isotropic pooling mechanism to combine V1 inputs. **However, if the maps were spatially uncorrelated (i.e., 'salt-and-pepper'), indiscriminate pooling would yield very little information.** Although all permutations of orientation and spatial frequency would also exist with salt-and-pepper organization, each downstream cortical cell would have to weigh its inputs in a far more complex and systematic manner to obtain diversity (see Figure 2 for a simple simulation to illustrate). Finally, it appears that a simple pooling mechanism can explain recent data on curvature tuning by V4 neurons [50]. The data show that curvature preferring V4 receptive fields contain local inhomogeneities in preferred orientation, reminiscent of orientation maps in V1 and V2.



Figure 2



Simulation to illustrate diversity of tuning via isotropic pooling from a continuous map. **(a)** Bottom image ('Input layer') is bandpass filtered noise to represent the map of an arbitrary response property. Each pixel value in the top image ('Output layer') is effectively an AND gate on local regions of the bottom map. Red pixels 'pool' from regions of the bottom map that have balanced distributions of input. Green pixels pool from regions that are more dominated by black or white. **(b)** Distributions of map values within the circled areas of the input map. **The clustering in the map creates diversity between the distributions.** **(c)** The bottom map was computed by taking the bottom map in (a), and randomly shuffling the pixels. The top map illustrates how indiscriminant convergent input from a salt-and-pepper map results in an emergent map with little information. **(d)** Local distributions are effectively all equal.

Rodent orientation 'maps'

Any model of the functional significance of feature maps has to address the fact that orientation tuning lacks an obvious organizational principle in rodent V1. **What could be the reason for this different form of organization?** First off, mouse LGN lacks the laminar architecture delineating pathways of On and Off cells [51,52] that is seen in animals with orientation maps [53–58]. **This likely contributes to the generous signal mixing of the different retinal ganglion cell types seen in the mouse [52,59].** In contrast, **the LGN segregation of parallel pathways in larger mammals may be the source of V1 clustering and thus maps [5,18**], as posited.** A second and related point is that much of the orientation tuning in mouse V1 appears to be inherited from earlier stages [52,59,60*,61]. In general, it stands to reason that building orientation tuning with such different circuits could generate different V1 maps. **Third, thalamocortical divergence is less pronounced in the rodent visual system than in larger mammals [62].** As a result, it can be expected that neighboring V1 neurons in the rodent will receive a relatively unique combination of inputs from the retina [62,63]. In summary, the presence of orientation maps may very well be contingent upon the evolution of two circuit properties: **laminar segregation in the LGN and thalamocortical divergence.** In turn, we may find that **a more important question than why maps exist in larger mammals is why evolution 'pushed' important computations downstream using strict laminar segregation of**

parallel processing streams. Allowing the expansive visual cortex to weave together the medley of parallel inputs — using maps — and systematically doing so across multiple serial stages is likely to provide computational advantages [64,65].

Future studies

There are, of course, many unanswered questions about V1 maps. A particularly important issue is the mutual relationship between orientation maps, On/Off maps, and retinotopy. For instance, if On/Off maps are analogous to the ocular dominance map in terms of their relationship to retinotopy [66], then we would expect retinotopic distortions at On/Off transition zones. However, these distortions may not be as dramatic if the On/Off maps are a reflection of the retinal mosaic [14**]. Next, there are multiple joint relationships between maps that to our knowledge cannot yet be accounted for by any circuit level model. Examples include the orthogonality between orientation and ocular dominance maps [15–17], orientation and spatial frequency maps [20**], and ocular dominance and disparity maps [10**]. Perhaps there are common factors giving rise to these relationships.

Although there is much work to be done, accumulating evidence points to a scheme whereby maps in V1 and other areas serve the purpose of setting up the next stage in the hierarchy. V1 maps are periodic [16,67], which means they will have repeating neighborhoods of tuning diversity from

which subsequent stages can pool to create the next stage of functionality. In this way, **emergent tuning properties at each stage may be seeded through maps of inherited tuning.**

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