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The Geometry of Visual Cortical Maps

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The primary visual cortex has a map of multiple visual parameters whose topographic relations remain poorly understood. A new study (Nauhaus et al., 2016) reveals a nearly geometric map-topography that coexists within a remarkably precise representation of visual space.

Imagine solving a puzzle that resembles a Rubik's Cube but with faces intersecting each other at different angles and compressed within a 2D sheet. Welcome to the primary visual cortex of primates and carnivores. Within a surface smaller than a credit card, the primary visual cortex is able to map a large number of visual parameters that include 2D spatial position, contrast polarity, ocular dominance, orientation preference, direction preference, and spatial frequency. Each of these parameters is represented smoothly within the cortical map so that neighboring values in parameter space are represented by neighboring regions in the cortex. How can all the different representations coexist without interfering with each other and causing map distortions that compromise vision? A paper in this issue of *Neuron* (Nauhaus et al., 2016) helps to solve the puzzle by showing that, while the cortical representation of visual space is remarkably precise, not all combinations of visual parameters are equally represented.

The representation of visual space in primary visual cortex of primates and carnivores is divided in columns of neurons that show preferences for different orientations and ocular dominance (Hubel and Wiesel, 1977). These columns are thought to be properly arranged to cover all possible stimulus combinations for each point of visual space. Therefore, orientation and ocular dominance change slowly throughout the horizontal dimension of the cortex along orthogonal cortical axes (Obermayer and Blasdel, 1993), as illustrated in Figure 1A. If orientation and ocular dominance were the only visual properties organized in columns, this orthogonal relationship could be enough to describe the organization of all stimulus combinations in the visual cortical map. However, multiple other parameters are also organized in columns, and while the number of columnar systems varies across animals, carnivores and primates have enough of them to keep scientists entertained for years to come.

In addition to orientation and ocular dominance, other map representations have been shown to intersect at orthogonal angles in visual cortex such as spatial frequency and orientation, and ocular dominance and retinal disparity (Kara and Boyd, 2009; Nauhaus et al., 2012; Yu et al., 2005). However, it is clear that not all parameter combinations can be accommodated with this strategy. The work of Nauhaus et al. (2016) now demonstrates an interesting example of a non-orthogonal map relation. By making multiple injections of Oregon green (a calcium sensitive dye) in the primary visual cortex of macaques, the authors were able to visualize relations among orientation, ocular dominance, and spatial frequency over cortical regions larger than the spatial period of the map, which is 0.5 mm. They show that, at least in non-human primates, spatial frequency and ocular dominance change in parallel along the same cortical axis (Figure 1B). Because spatial frequency and ocular dominance have to maintain the same periodicity throughout the cortex, the map cannot represent all combinations of spatial-frequency and ocular dominance equally. The high-quality data obtained by Nauhaus et al. (2016) convincingly show that monocular regions at the center of ocular dominance columns have a preference for low spatial frequencies and binocular regions at the border of ocular dominance columns have a preference for high spatial frequencies. This topographic arrangement indicates that the visual cortical map devotes more neuronal resources to represent binocular stimuli with high spatial frequency than low spatial frequency. It would be surprising if this topographic relationship
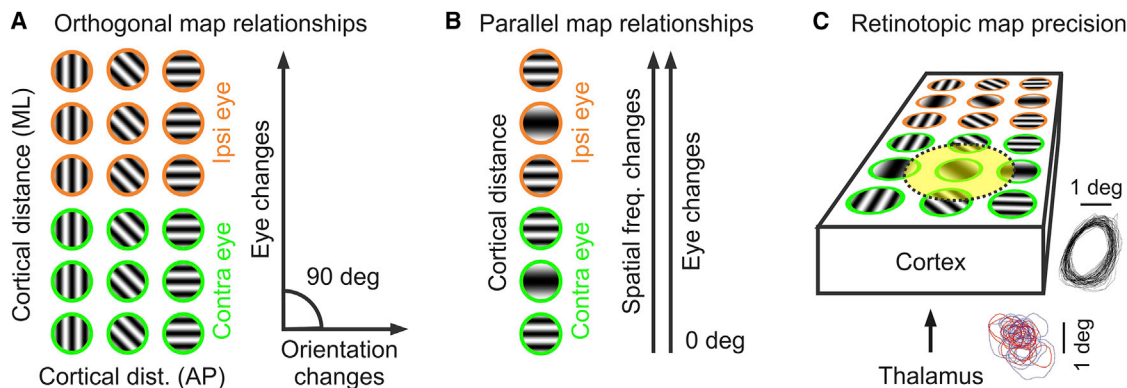
Figure 1. Cortical Map Relationships for Different Features of Primary Visual Cortex
(A) Left: Cartoon illustrating the stimulus preferences of a rectangular sheet of cortex. Stimulus orientation changes from vertical (left) to horizontal (right) across the antero-posterior axes (AP) of the cortex and ocular dominance changes from contralateral eye (contra, green) to ipsilateral eye (ipsi, orange) across the medio-lateral (ML) axes. Each circle represents the stimulus preferences of a cortical point in cortex and are separated from each other by 0.25 mm of cortical distance. Right: The gradient of changes for orientation and eye dominance intersect at a 90° angle.
(B) Cartoon illustrating the new discovery from Nauhaus et al. (2016). Changes in spatial frequency occur in parallel with changes in eye dominance across the same cortical axis.
(C) Cartoon illustrating changes in orientation preference (x axis), eye dominance and spatial frequency (y axis) that coexist with a precise representation of visual space. The yellow circle illustrates a region of cortex of approximately 0.2 mm diameter in which receptive field position remains nearly constant as illustrated by the cortical receptive field outlines (black) measured by Nauhaus et al. (2016) in macaques. This spatial precision is likely to reflect the retinotopic precision of the ON (red) and OFF (blue) thalamic inputs feeding the cortical region marked by the yellow circle, which was measured by Jin et al. (2011) in cat visual cortex.

did not have consequences for the computation of retinal disparity and binocular vision; however, we will have to wait for further research to understand its possible functional implications.

How common are these biased sensory representations in visual cortical maps? Map organization differs greatly across animals. For example, ocular dominance is horizontally segregated throughout the cortex in macaques, cats and ferrets but vertically segregated in tree shrews. Also, visual cortical maps in rabbits (as in mice and rats) lack segregation for both ocular dominance and orientation even if the size of the visual cortex is just as large in rabbits as in ferrets. While parameter segregation varies across animals, representation biases may be a constant property of cortical topography in mammals. Cortical maps are not Google maps and do not use the same scale to represent different regions of visual space. Instead, the cortical representation of sensory space is heavily distorted to optimize neuronal resources based on visual needs. For example, in animals with good visual acuity, the representation of central vision occupies a much larger portion of the visual cortex than the representation of the visual periphery and darks are represented with more spatial precision than

lights (Kremkow et al., 2016; Lee et al., 2016). These biases in cortical topography explain why visual acuity is highest in central vision and why we prefer to read dark characters in bright background like the text in this page. Visual cortical maps are also biased for cardinal orientations; the contralateral eye; and, as Nauhaus et al. (2016) shows, for binocular high spatial frequencies.

Nauhaus et al. (2016) also demonstrate that, while visual cortical maps do not provide a balanced representation of all stimulus combinations, they have an exquisite representation of spatial position. Just as the resolution of a computer monitor can be improved by increasing the number of pixels and reducing pixel size, cortical maps can improve visual resolution by increasing the number of cells and reducing receptive field size. However, the monitor resolution can easily deteriorate if the value of each pixel is spatially scattered, even if the scatter is small. The primary visual cortex does not take any chances and strongly limits receptive field scatter. The work of Nauhaus et al. (2016) demonstrates that the receptive field scatter within a region of 0.2 × 0.2 mm of primate visual cortex is as close to zero as it can be (Figure 1C). This finding nicely agrees with the limited receptive field scatter of

thalamic inputs feeding the same cortical orientation column, which has been shown to match the size of a cortical receptive field in cat visual cortex (Jin et al., 2011). The receptive field position also changes slowly across horizontal cortical distance, maximizing the representation of different stimulus combinations for each point of visual space. However, the individual ON and OFF subregions within the receptive field may show abrupt spatial changes within small cortical distances, which relate to changes in orientation and direction preference across the cortical map (Kremkow et al., 2016; Lee et al., 2016).

The results from Nauhaus et al. (2016) are a major step toward understanding how different visual parameters are represented in the cerebral cortex. However, there is still a long road ahead until we fully understand the functional organization of visual cortical maps. Technical limitations in the past have sometimes led us to believe that cortical architecture is sloppy, receptive field scatter is large and parameter representations within cortical maps are weakly related. However, after Nauhaus et al. (2016), cortical maps are beginning to look more like a geometrical puzzle than a fuzzy mosaic. The future research of cortical cartography looks very exciting and the

combination of more accurate experimental measurements (Kremkow et al., 2016; Lee et al., 2016; Nauhaus et al., 2016) and computational models (Miller, 1994; Paik and Ringach, 2011; Swindale et al., 2000) may soon explain what we thought were complicated parameter relations with some simple connectivity rules.

A better understanding of visual cortical topography is likely to bring important new insights about cortical function. Knowing what and how image parameters are mapped in visual cortex and what parameter combinations are allocated the largest portion of cortical space can help to better understand the building blocks of visual cortical processing. Parameters that are mapped together may be more likely to be wired together in the form of local and long-distance neuronal networks, and knowledge of this topography may help to reveal new rules of cortical connectivity. Visual cortical maps are also closely related to visual

function. For example, humans maximize the visual processing of detail and color by dedicating half of their primary visual cortex to a small fraction of their central retinas while using the rest of the visual cortex to map the binocular visual field. In contrast, rabbits maximize their chances of survival by devoting a large portion of their visual cortex to a horizontal retinal line that help them detect distant predators, while using the rest of their visual cortex to nearly cover a complete visual-field-sphere surrounding their heads. Just as the differences in spatial mapping are closely related to visual function, future research may reveal the functional implications of specific topographic relations that remained hidden by our coarse technical tools.

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Neuronal Mechanisms and Transformations Encoding Time-Varying Signals

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Sensation in natural environments requires the analysis of time-varying signals. While previous work has uncovered how a signal's temporal rate is represented by neurons in sensory cortex, in this issue of *Neuron*, new evidence from Gao et al. (2016) provides insights on the underlying mechanisms.

The song of the cricket and repetitive drumming of a woodpecker are examples of natural time-varying signals created by the periodic repetition of transient acoustic events (Figure 1A). Perceptually, we hear each woodpecker's peck as a discrete event, while the repetitive leg-wing rubbing that produces the cricket song is perceptually fused into a single continuous sound (compare Audio S1 and S2, available online). Why we perceive

slowly repeated sounds as discrete events (flutter perception) and quickly repeated sounds as a continuous acoustic signal (fusion perception) is thought to be a direct result of how these signals are represented by sensory cortical neurons.

The temporal rate of a sensory signal is initially represented in the sensory periphery by a stimulus-locked temporal firing pattern. However, as signals ascend the

auditory, somatosensory, or visual processing pathways, neurons progressively worsen in their temporal fidelity. In the auditory system, for example, although auditory nerve fibers can synchronize their responses to temporal rates above 1 kHz, this upper cut-off of stimulus synchronization decreases at hierarchically higher auditory areas, falling to around only 30–50 Hz in primary auditory cortex (Joris et al., 2004; Wang, 2007). Moreover,