Organization of Orientation-Selectivity in Cat Primary Visual Cortex: The Winding Path to Pinwheels

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March, 2025

Since Hubel and Wiesel's pioneering studies beginning in the 1950's, our understanding of the organization of primary visual cortex (V1) has undergone several refinements. This report will outline the development of our understanding of the organization of orientation-selective cells in cat primary visual cortex, culminating in Bonhoeffer and Grinvald's intrinsic signal optical imaging (ISOI) [3] measurements, which showed that orientation-selective columns of cat V1 are organized in "pinwheel-like" patterns [1].

1 Electrophysiology Suggested Spatially Structured Orientation-Selectivity in Cat and Macaque V1

Hubel and Wiesel's electrophysiology experiments laid the foundation for understanding the organization of the early visual system. In these experiments, long, thin electrodes are inserted into the exposed brains of anesthetized animals, and local field potentials are recorded while visual stimuli are presented to the animal. When probing the visual fields of cat primary visual cortex (V1), Hubel and Wiesel would make an astounding discovery: unlike the center-surround receptive fields common to cells in the retina an the Lateral Geniculate Nucleus, most cells in V1 were selective to stimuli of a particular *orientation* [4]. This orientation-selectivity remains a hallmark of V1 organization.

While Hubel and Wiesel's single-electrode recordings were constrained to measure only a few neurons simultaneously, they were still able to make some deductions about the organization of orientation-selective neurons within V1. In one set of experiments, they insert an electrode into cat V1 and probe for the stimulus orientation that evokes the maximum response from the recorded cells [5]. As the measuring electrode penetrates deeper into the visual cortex, it will record the local field potentials of correspondingly deeper neurons. When the electrode was inserted perpendicular to the cortical surface, orientation-selectivity changed little or not at all with increased depth [5]. However, when the electrode penetrated at oblique angle, orientation selectivity changed at a much greater rate (See Fig, 1A). These experiments suggested that cells in V1 are organized into columns which share their orientation selectivity. Additional experiments in macaque V1 [6] showed that when the electrode penetrates tangentially to the cortical surface, orientation selectivity undergoes wide swings in its rate of change, as well as abrupt jumps. They concluded that orientation-selective columns are "highly ordered and probably have the form of parallel slabs" [6]. Meanwhile, other investigators sought a more principled explanation of these measurements. In particular, Braitenberg and Braitenberg, suggested that the rapid changes and abrupt jumps in orientation selectivity in Hubel and Wiesel's recordings could be explained by orientation columns organized in the "pinwheel" pattern shown in Fig 1B [2].

2 2-Deoxyglucose Imaging Experiments Suggested Linear Organization of Orientation-Selective Columns

Löwel et al. used 2-Deoxyglucose (2-DG) imaging [9] to visualize orientation-selectivity columns in

cat visual cortex [8]. In these experiments, cats are injected with a radioactive isotope of Glucose, then shown visual stimuli consisting of gratings of a particular orientation. During this time, neurons with increased metabolic activity will take up radioactive glucose from the bloodstream at a higher rate than inactive neurons. After tens of minutes, the cats are sacrificed, their visual cortex unfolded into a sheet, and the pattern of orientation-selective neurons visualized using autoradiagraphy. Unlike electrode recordings, 2-DG imaging can map the activity of a whole patch of cortex. However, the resulting images show activity accumulated over all stimuli presented between injection and sacrifice. Most of Löwel et al.'s experiments therefore obtained cortical maps of the cells responsive to visual stimuli of a single orientation. For example, Fig. 2A, shows cortical columns in cat V1 and V2 selective to vertical contours. Orientation-selective columns appear to join together into beaded "stripes." Similar experiments conducted by Hubel et al. concluded that orientation columns are organized in "swirling stripes with many bifurcations and endings" [7].

Despite the limitations of 2-DG imaging, Löwel et al. devised an experiment which attempted to distinguish between the "swirling stripes" organization proposed by Hubel and Wiesel, and the "pinwheel" organization proposed by Braitenberg and Braitenberg. In a single trial, they showed a cat visual stimuli which alternated between vertical and horizontal orientations. If orientation-selectivity columns were arranged in pinwheels as predicted by Braitenberg and Braitenberg, they reasoned, the resulting pattern on the cat's visual cortex should consist of perpendicular stripes. However, they instead observed that all adjacent stripes were arranged in parallel (Fig. 2B). Reasonably, they concluded that cat V1's orientation selective columns were most likely organized into parallel stripes rather than pinwheels. In section 3, we will see that more precise measurements indeed do find a pinwheel architecture in cat V1, and in section 4 we will discuss how to reconcile these seemingly contradictory observations.

3 Intrinsic signal optical imaging permitted an unambiguous demonstration of pinwheels

Electrophysiological recordings allowed extensive mapping of single-neuron receptive fields and 2-DG imaging permitted limited mapping of receptive fields over large patches of cortex. In order to determine the *relative* organization of the columns sensitive to *different* orientations, experimenters needed to record from a patch of cortex *during* the presentation of multiple stimuli in succession. Intrinsic signal optical imaging (ISOI), introduced in 1986 [3], provided precisely this capability.

ISOI leverages the fact that changes in local metabolic processes, such as increased blood flow or oxygenation, change the reflectance of neural tissues. By comparing images taken before and after stimulus presentation, one can map the functional architecture of patches of cortex *during* stimulation. Bonhoeffer and Grinvald revisited orientation-selectivity in cat visual cortex using ISOI [1], recording activity in V1 upon presentation of stimuli of many orientations. When the cells responsive to any given orientation are visualized, beaded patterns similar to those obtained using 2-DG imaging are recovered (Fig. 3a,b). However, when the different orientations are combined into a single map showing the orientation of *maximum* response, it immediately becomes clear that the orientation-selective columns are organized into "pinwheel-like" patterns which are centered on vertices lacking orientation selectivity (Fig. 3c).

4 Discussion: Why did Löwel et al. miss the pinwheels?

So, how do we square Bonhoeffer and Grinvald's unambiguous demonstration of pinwheel-like organization with Löwel et al.'s evidence in support of a parallel stripe model? Comparing their

results retrospectively, an amusing explanation comes into view. To understand this discrepancy, we first examine the pinwheel-like structures predicted by Braitenberg and Braitenberg. When rotating about the center of a pinwheel from Fig. 1B, the preferred orientation rotates through a full 360 degrees. However, in the pinwheels ultimately observed in cat V1 [1], preferred orientation rotates through 180 degrees in the 360 degrees around each pinwheel. This scheme reflects the rotational symmetry of a bar-shaped stimulus, for which orientations of 180-360 degrees are equivalent to orientations of 0-180 degrees. Whereas the pinwheels predicted by Braitenberg and Braitenberg contained these duplicate representations of the orientations, the pinwheels observed in cat V1 do not contain these duplicates. Consequently, the angle between the stripes measured on the cortical surface will be scaled up by a factor of two relative to the angle between the orientation of two stimuli. Unfortunately, Löwel et al. based their experimental design on the incorrect presumption of a 360 degree orientation change per rotation about each pinwheel center. Hence, they expected vertical and horizontal stimuli to activate *perpendicular* stripes in the visual cortex (see Fig. 4A). However, under the (true) 180 degree orientation change, vertical and horizontal stimuli would activate parallel stripes of beads (see Fig. 4B), which is precisely what Löwel et al. observed! This led them to the erroneous conclusion that orientation-selective columns were organized into parallel stripes corresponding to different orientations. In retrospect, a small modification could have pointed Löwel et al. in toward the right conclusion – had they measured the patterns of cortex selective for two stimuli which were offset by 45 degrees, they would have seen a perpendicular grid of stripes (fig. 4C). This would have contradicted the parallel stripe hypothesis, and suggested the presence of pinwheel organization with 180-degrees of orientation change per pinwheel.

5 Conclusion

As experimenters developed electrophysiology, 2-DG imaging, and ISOI, our understanding of orientation-selective columns in cat V1 improved dramatically. Importantly, ISOI permitted an unambiguous demonstration that orientation-selective columns are organized into pinwheel-like structures with a periodicity of 180 degrees. The conclusions reached by [8] provide a salient example of how the preconceived notions of experimenters may lead them to an incorrect interpretation of their data. And, as new technologies permit more detailed experimental measurements, seemingly contradictory findings of previous experiments can often be reconciled within a unifying framework. In this case, measurements made with ISOI demonstrated that the columns of orientation-selective neurons in cat V1 are organized into pinwheel-like structures, with selectivity sweeping through 180 degrees of orientation change per 360-degree rotation about each pinwheel center. Under a single umbrella, these observations were able to explain the rapid jumps in orientation selectivity observed in Hubel and Wiesel's electrode recordings, and the parallel beaded stripes responsive to individual, or perpendicular, orientations observed using 2-DG imaging [4, 8].

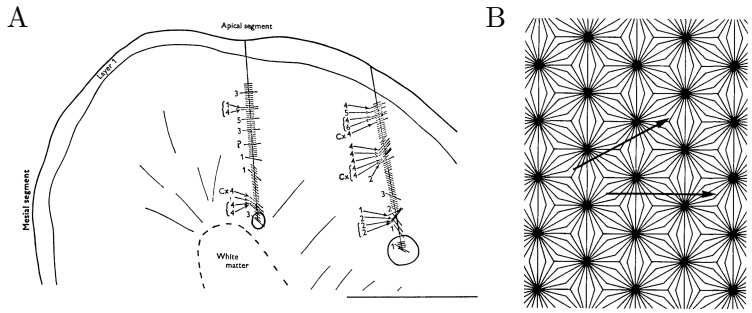

Figure 1: (A) Schematic showing orientation-selectivity measurements made in cat V1. The orientation eliciting the strongest response is determined for neurons at increasing depth from the cortical surface. When the electrode punctures perpendicular to the cortical surface, orientation changes are slow. When the electrode enters at an oblique angle, orientation changes quickly, and can undergo abrupt jumps. Figure taken from [5]. (B) "Pinwheel" organization of orientation-selective columns proposed by Braitenberg and Braitenberg on the basis of electrophysiology recordings made in [6]. Lines represent the orientation-selectivity of cortical neurons. Note that orientation-selectivity sweeps through 360 degrees during a rotation about each pinwheel center.

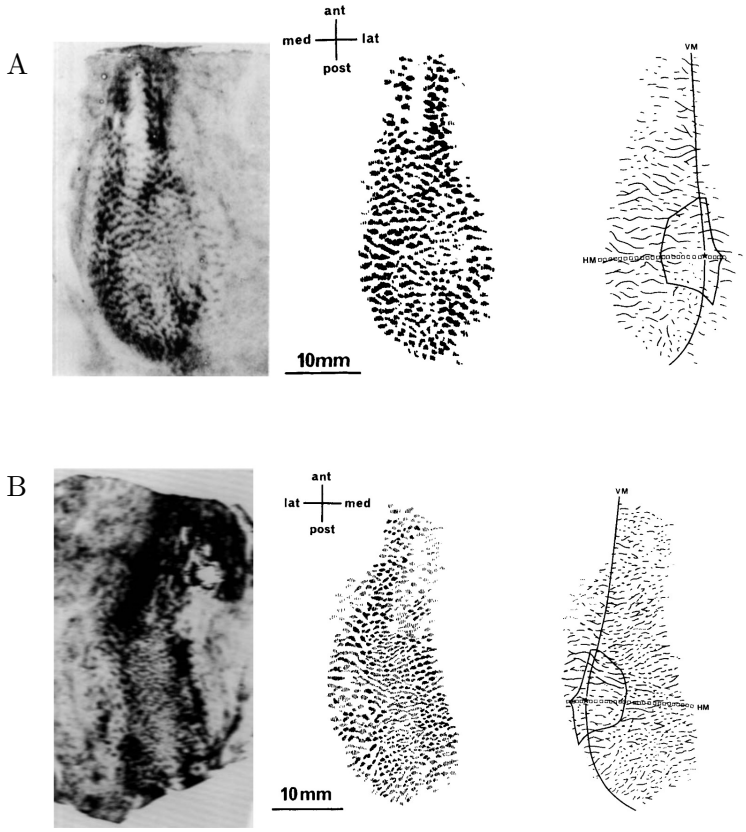

Figure 2: 2-Deoxyglucose imaging of Cat V1 and V2 from [8] after presentation of (A) vertically oriented stimuli and (B) both vertically an horizontally oriented stimuli. Left: autoradiographs. Center: hand drawings of "beads" in the autoradiograph. Right: Drawn contours connecting the centers of adjacent beads showing a parallel stripe organization in both cases. VM, vertical meridian; HM, horizontal meridian.

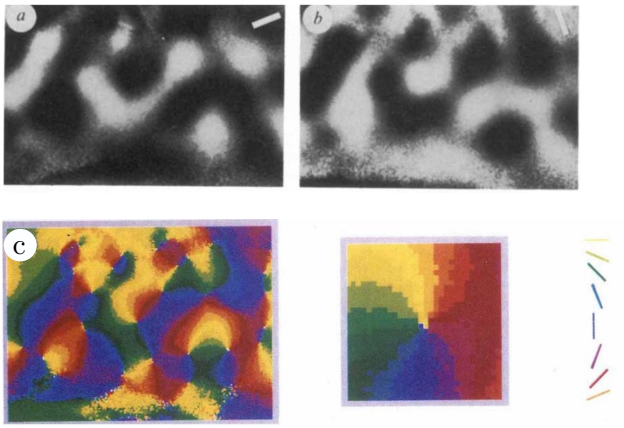

Figure 3: Intrinsic Signal Optical Imaging of cat V1 demonstrates pinwheel structure of orientation selective columns. (a,b) ISOI recordings of a patch of V1 in response to stimuli of a single orientation (shown top right) produce beaded patterns similar to 2-DG imaging. (c) Map of the same region showing the orientation which elicits the maximum response. Right shows an expanded view of a single pinwheel center. Figure taken from [1]

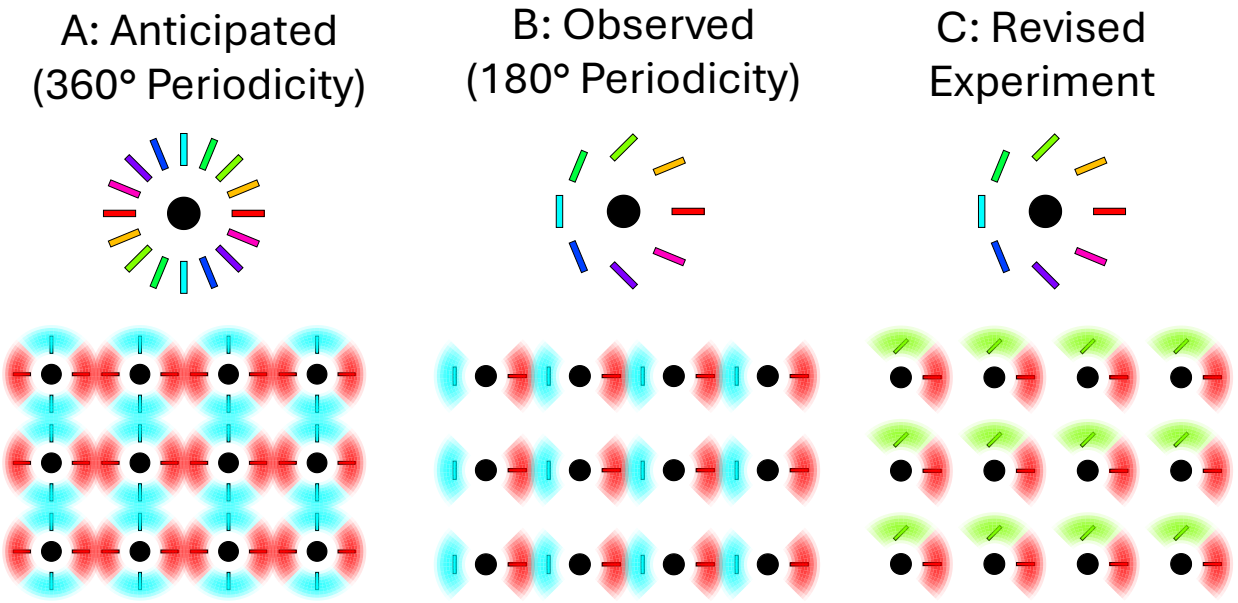

Figure 4: Diagrammatic explanation of the experimental findings of in 2-DG imaging experiments [8]. (A) Under the presumption of 360 degree sweep in orientation selectivity per rotation about each pinwheel center, the presentation of horizontal and vertical simuli should have evoked perpendicular stripes of activity in visual cortex. (B) Under the true pinwheel design of a 180 degree sweep in orientation selectivity per pinwheel rotation, presentation of horizontal and vertical stimuli should elicit parallel stripes of responsive neurons in V1. This is consistent with observations in Fig. 8 from [8], reproduced in Fig. 2B. (C) Anticipated results of a revised 2-DG imaging experiment in which stimuli with horizontal and oblique orientations are presented. With the correct 180 degrees per pinwheel rotation, stimuli offset by 45 degrees should elicit beaded stripes that are offset by 90 degrees on the cortical surface.

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