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Integrated Sciences

The Visual Cortex

The paper, “An Evolution of Ideas on the Primary Visual Cortex, 1955-1978: A Biased Historical Account” is an account of the series of experiments done by David Hubel and Torsten Weisel. Their experiment began as an attempt to come up with a method to consistently cause cells in the visual cortex to fire using visual stimuli so that the structure and workings of the visual cortex could be better understood. They started their experiment in Kuffler’s laboratory, whose theories about on-center and off-center retinal ganglion cells (based on the center-surround idea first discovered by Vernon Mountcastle in the somatosensory cortex, which said that the receptor cells had small circular regions of excitatory and inhibitory fields) they decided to use by applying them to the visual cortex. However, previously Hubel was having difficulty in getting the cells to fire because they were very insensitive to diffuse light, unlike the ganglion cells in Kuffler’s experiments, and could only slightly affect some cells by the use of small circular stimuli projected on a screen, but still failed to have any effect on many cells. Clearly the classic center-surround model used in Mountcastle and Kuffler’s experiments was not entirely applicable to the visual cortex.

The first time they made real progress on the cortical cells was actually an accident. One day during an experiment they were inserting a slide with a black dot and realized they were getting more responses than they normally would at obscure locations, eventually realizing that it was the edge of the glass slide creating a thin line on the projector screen which caused the cat’s cells to fire. They had realized that something was different about the primary visual cortex and its cells from the retinal ganglion cells of Kuffler’s experiment and the lateral geniculate cells, which Hubel was already convinced were center-surround as well, but this was essentially the first hint as to how the cortical cells worked and what they were for.

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After further investigation into the implications of this finding, they began testing on the cortical cells again, but this time using bars of light as stimuli. It became clear that each cell was sensitive to edges, but that each cell responded to edges of only one particular orientation. They then came to the conclusion that there were different cell set types in the visual cortex based on the range of reactions they received from stimuli. The most basic type they named simple cells. These cells are sensitive only to stimuli of a specific orientation and position in the receptive field. They have excitatory and inhibitory regions just as a center-surround cell would, but the center is a set of parallel lines instead of a spot, and the inhibitory regions surround that bar. Each cell has a very specific orientation and only responds to stimuli within a very small angular and positional range. Stimuli parallel to the orientation of a cell elicited no response at all, as did diffuse light, because the responses from the excitatory and inhibitory regions seemingly cancelled each other out. However, some cells were sensitive to movement, unlike the simple cells, and these they called complex. However, these have just as restrictive an orientation as simple cells; they just have a larger receptive field and a directional sensitivity. This led them to believe there was a hierarchy within the cells and that the complex cells received input from multiple simple cells, allowing the complex cell to sense motion as the stimuli moved from one simple cell to another. Assuming this were true, the complex cells would only be sensitive to motion perpendicular to its orientation and not to parallel movement. This also was true, the direction of movement was very crucial in activating the complex cells, and stimuli moving in the correct direction would cause the cells to fire at a very high rate. Finally, they discovered what they called the hypercomplex cells (which recently have been renamed to complex end-stopped cells), which were sensitive to movement and orientation, but added another dimension to the inhibitory field. This meant that not only did the width of the stimuli matter, but the length also mattered. Thus, if they used a very long bar, the cell would not fire as much as if they used a bar closer to the ideal length. This function is what allows for detection of corners in the visual field. Thus, they assumed that these hypercomplex cells must receive input from multiple complex cells. However, if this were the case, there would be different orientations of complex cells, and therefore a hypercomplex cell should be sensitive to motion in more than one direction. However, like a complex cell, it can only sense direction in one motion, meaning it, too, must be connected to simple cells and this is why the name was changed to complex end-stopped.

They also made many discoveries in their experiments which have contributed greatly to the modern understanding of the architecture in the visual cortex. Histology was a very important part of their experiment throughout, not only because they obtained a histological technician, but also because of the method of making electrolytic lesions developed by David Hubel. During their penetrations into Section V1, after some experimentation, they came up with a method in which they would alternately record the output of a cell and send a small electrical impulse to that section of the brain, causing a small lesion. Then, when doing the histology later, this would allow them to see exactly where it was in the brain that they were recording and map out the results. They were hoping to find columns similar to those discovered by Mountcastle in the somatosensory cortex. In one recording on the striate cortex of a monkey, they realized how true their suspicions were when they were getting orientations which gradually progressed by angle as they penetrated deeper. They did many such experiments and found that the majority of the time, the orientation of the cells progressed like this in an orderly fashion, albeit with seemingly random reversals in the change in orientation. There were very rarely large jumps in the angle of orientation, and even when going through layer IVc there was no interruption, even though theoretically the cells in that layer are not orientation specific (this was something that they could not explain, and it is still unknown why they obtained such results). After many penetrations and mappings, they concluded that cells were grouped according to orientation and neighboring cells had slightly different positions in the receptive field. Also, they realized that these columns contained the hierarchy of cells within them, that the connections between simple and complex cells were all within the same column.

Another important discovery was the idea of ocular dominance columns. They realized that the cells in the lateral geniculate nucleus were monocular, receiving input from only one eye, whereas the majority of cortical cells were binocular. This of course led to questioning as to how and when cells first received convergent input from the two eyes. After close examination of the binocular cells in the cortex, the discovery of “eye preference” or “relative ocular dominance” in these cortical cells followed. Hubel and Wiesel noticed in the early experiments involving the macaque that adjacent cells have similar eye preferences and in vertical penetrations through the cortex the preference is all the same, hinting at ocular dominance columns, up until layer IVc where cells are purely monocular with sets of identical cells, otherwise known as terminals, grouped together evenly. They concluded that these terminals in IVc receive all of the information from the lateral geniculate first and then forward it to the rest of the cortex, translating it to binocular. Also, the terminals are arranged and linked to the lateral geniculate based on their eye of origin in an alternating fashion. Using fundamentally the Nauta method and making lesions, they were able to stain and view the distribution of terminals. Upon reading that a radioactive amino acid injected in the eye could be detected in the cortex via an autoradiograph, Hubel and Wiesel ultimately used this method to map ocular dominance columns with much greater efficiency than by the Nauta method, thus accomplishing one of their key goals.

Integrated sciences are seen throughout the paper in Hubel and Wiesel’s experimental methods and more generally, neuroscience. In the field of neuroscience, the integration of various sciences has been responsible for the incredible advances seen in the last several decades. As seen in the paper, neuroscience involves anatomy, biochemistry, optical physics, and molecular/cellular biology. Cellular biology and anatomy play the largest role in the experiment, a key example being their use of the altered Nauta method and other histological methods in order to map the ocular dominance columns and other parts of the brain. Also, the gadgetry and the associated methodology that Hubel and Wiesel employed incorporate electrical science in the use of electrodes, scientific technology, and add more facets to the aspects of cellular biology.