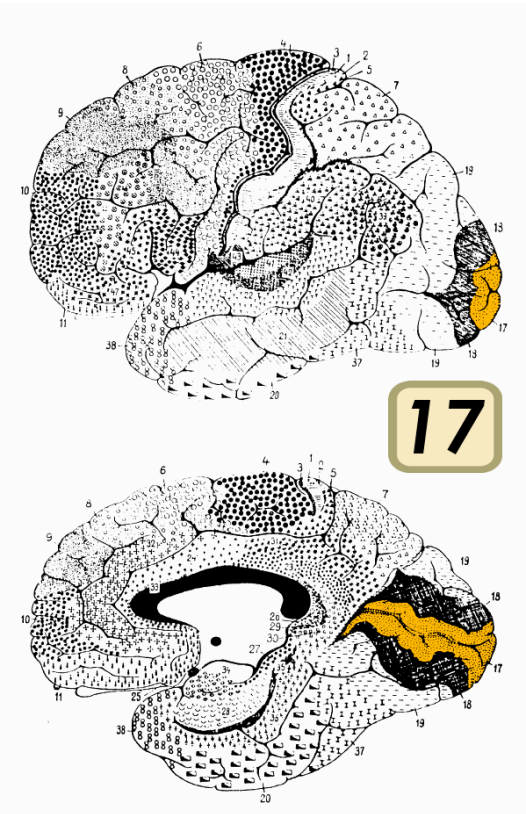
Chapter V. Primary visual cortex

The main output projection from the lateral geniculate nucleus (LGN) conveys visual information to primary visual cortex. This is not the only LGN output but it is considered to be the key pathway for visual object recognition. Primary visual cortex is also known as area V1 or striate cortex[1]. Primary visual cortex is the first stage where information from the two eyes converges onto individual neurons. It is also one of the most heavily studied parts of cortex.

5.1. About neocortex

Figure 5.1: Brodmann subdivided neocortex into multiple areas based on cytoarchitectonic criteria. Primary visual cortex (Brodmann area 17) is marked in orange in this diagram [source = Wikipedia].



The human neocortex is about 2-4 mm thick; it is characterized by multiple convolutions such that it can fit about 2600 cm^2, about half a basketball court. The German neuroanatomist Korbinian Brodmann devised a parcelation of the human and monkey brains – as well as many other species -- based on morphological cytoarchitectonic criteria. To this days, many parts of neocortex are still referred to by their Brodmann area number (**Figure 5.1**) (Brodmann, 1909). Subsequent physiological and lesion studies have shown that many of these structural subdivisions correlate with functional differences. Localization of brain function has a long and rich history that continues to current days (Finger, 2000). Primary visual cortex corresponds to Brodmann's area 17.

5.2. Connectivity in primary visual cortex

[1] In the cat literature, primary visual cortex is also referred to as area 17.

Primary visual cortex receives direct input from the lateral geniculate nucleus. Each hemisphere in V1 represents the contralateral visual field. The part of the retina that is closer to the nose is called nasal while the other half of the retina is called temporal. The left visual field (left of where the eyes are fixating on) is represented by the nasal part of the retina on the left eye and by the temporal part of the retina on the right eye. Information from the nasal retina on the left eye will cross the brain and end up represented in the right hemisphere. Information from the temporal retina on the right eye will turn at the optim chiasm and also end up represented in the right hemisphere.

Figure 5.2: Visual deficits obtained from gunshots as mapped by Holmes [source=British Journal of Ophthalmology (1918) 2:353-384].

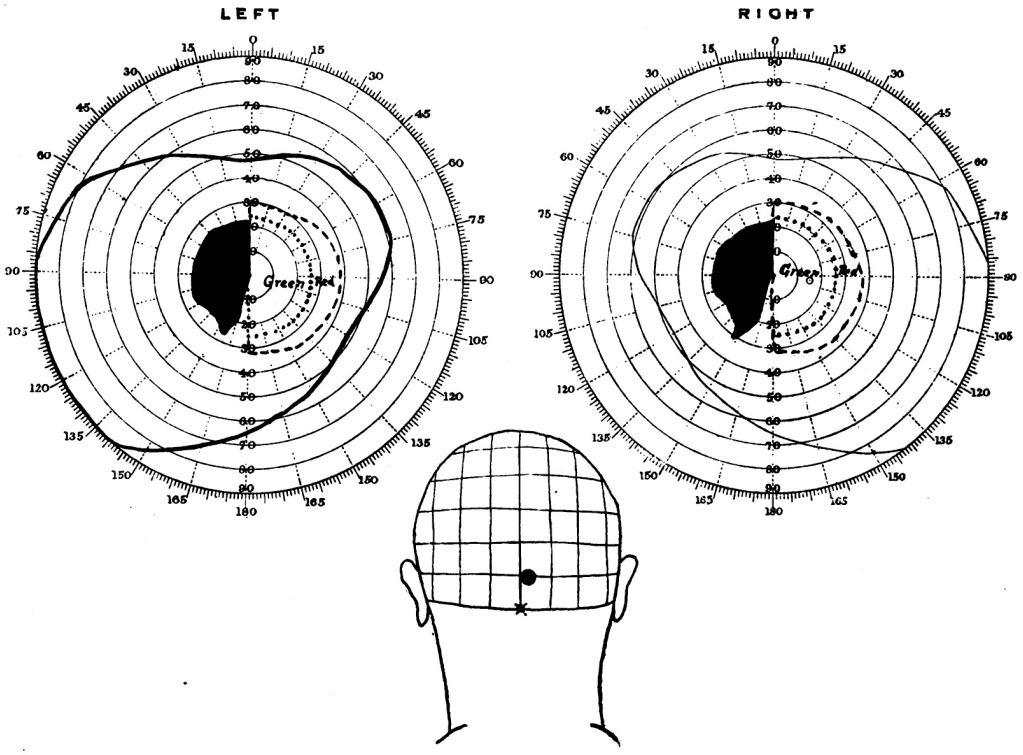


FIG. 1.

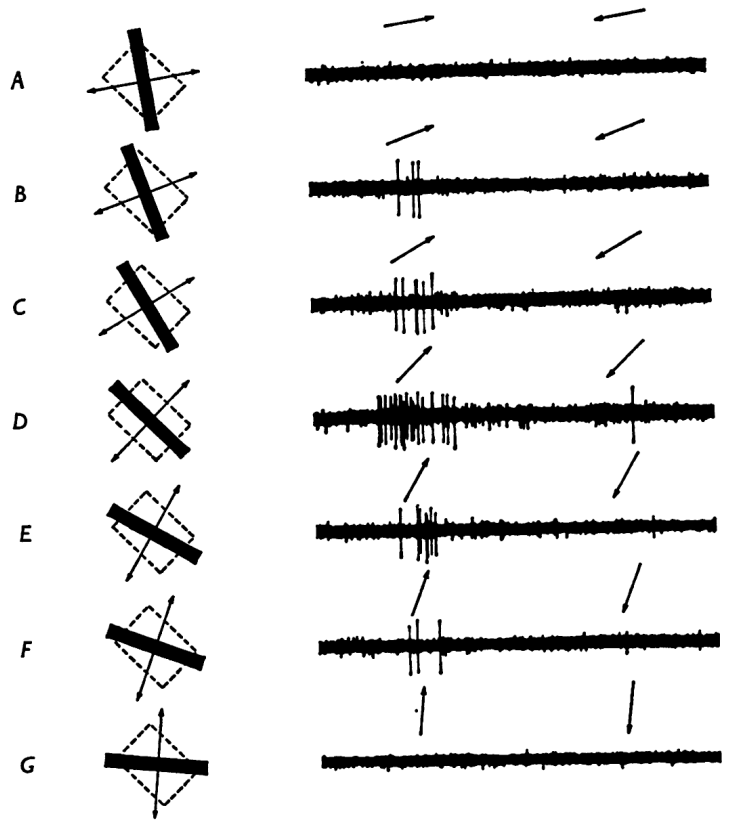
Like most other aspects of neuroanatomy, the first drawings of primary visual cortex were made by Santiago Ramon y Cajal. Primary visual cortex has a stereotypical architecture that is, to a coarse approximation, similar to that of other parts of visual neocortex. The neocortical sheet is characterized by six layers that can be distinguished in a Nissl staining. These layers are characterized by a typical connectivity pattern that is often referred to as the canonical microcircuit. With some exceptions (it is biology after all), this canonical connectivity pattern is shared across different visual areas and also across

different sensory modalities. The LGN projects to pyramidal cells in layer 4 in primary visual cortex, perhaps the most studied layer. Connections among different areas of cortex are often described as "bottom-up", "top-down" or "horizontal" connections. These different connections can be defined based on the specific layer of the pre- and post-synaptic neurons. Bottom-up connections arrive at layer 4. Layer 1 is the most superficial layer and contains mostly dendrites and few cell bodies, which are mostly located in layers 2 and 3. Top-down connections from other visual cortical areas (particularly so-called area V2) typically end in the deep layers 5 and 6 (Felleman and Van Essen, 1991) and also to a lesser degree in layers 2 and 3. After thalamic input arrives onto layer 4, information flows from layer 4 to layers 2/3 and then onto layer 5. Information from layer 6 provides backprojections to the LGN and is also fed back to layer 4. Layers 2/3 project to layer 4 in higher visual areas.

By scrutinizing these interlaminar connectivity patterns in multiple brain areas, investigators have come up with an approximate map of how different visual areas communicate with each other. The interlaminar connectivity also helps place two interconnected visual areas in terms of which one provides bottom-up inputs and which one provides top-down signals. This led Felleman and Van Essen to build the now famous map of mesoscopic interconnectivity of visual cortical areas (Chapter 1). With rare exceptions, essentially every cortical area A that send bottom-up signals to an area B also receives top-down projects from B to A. By virtue of defining what is bottom-up and what is top-down, the Felleman and Van Essen diagram provides a semi-hierarchical description of the anatomical flow of information in the visual system. This semi-hierarchical architecture has played an important role in inspiring the development of deep architectures as computational models for vision (Chapter 8).

3.2 How to study neuronal circuits

Figure 5.3: Example showing responses of a neuron in primary visual cortex to bars of different orientation. In these examples, the bar was moved in a direction perpendicular to its orientation. The dashed lines on the left indicate the receptive field, the black rectangle is the oriented bar and the arrows indicate the direction of motion. The neuronal response traces are shown on the right. [Source = Journal of Physiology (1968) 195: 215-243]



Every problem has an appropriate scale of study, a Goldilocks scale, not too coarse, not too fine. For example, it is particularly tedious and difficult to attempt to read the newspaper using a microscope (too fine a resolution) or from a distance of 20 meters away (too coarse). In the case of neocortical circuits, this Goldilocks scale is given by examining the activity of individual neurons. Studying the three-dimensional structure of each protein inside a neuron is equivalent to trying to read the newspaper with a microscope (but it can be extremely useful for other questions such as understanding the kinetics and properties of ion channels in the neuronal membrane). Studying the average activity of a cubic centimeter of cortex is equivalent to attempting to read the newspaper from 20 meters away (but it can be extremely useful for other questions such as differentiating general properties of a part of cortex). In addition to this spatial scale, there is also a natural time scale to examine neuronal activity. Neurons communicate with each other by sending electrical signals called action potentials (Kandel et al., 2000)[2] lasting a few milliseconds. For most purposes, it is sufficient to study neuronal activity at the millisecond level. With a few exceptions (e.g. small differences in timing between signals

[2] A few neurons only show graded voltage responses and do not emit action potentials.

arriving at the two years), microsecond resolution does not provide additional information and averaging activity over seconds is too coarse.

Studying the activity of neocortical circuits at neuronal resolution is not trivial. The gold standard is to examine the activity of individual neurons at millisecond resolution by inserting thin microelectrodes. Neuronal action potentials lead to changes in the electrical potential in the extracellular milieu. With appropriate equipment, it is possible to amplify and measure this electrical potential in the extracellular milieu and measure the action potentials emitted by individual neurons. The methodology was established by Edgar Adrian (Adrian, 1926).

5.3. Nearby neurons show similar properties

The primary visual cortex is about 2 mm thick and the entire surface is a few square inches in surface. There are about 200 million cells in primary visual cortex. As discussed in the previous chapter, neurons in primary visual cortex (as well as other parts of visual cortex) show spatially restricted receptive fields, that is, they respond to only a certain part of the visual field. The receptive field size of neurons in primary visual cortex is larger than the ones in the retina and LGN and can typically encompass about 1 degree of visual angle.

The connections from the LGN to primary visual cortex are topographically organized, meaning that nearby neurons in the LGN map onto nearby neurons in primary visual cortex. Nearby neurons in the LGN in turn typically have adjacent and typically overlapping receptive fields. Thus, primary visual cortex is also retinotopically organized, meaning that nearby neurons have receptive fields that map onto nearby parts of the visual field and of the retina.

5.4. Lessons from the war and gunshots

Local damage in primary visual cortex gives rise to blind regions in the visual field (“scotomas”). To a first approximation, the effects are similar to the ones observed due to local lesions in parts of the retina. The initial discovery of primary visual cortex as a light-sensitive area can be attributed to the study of neurological deficits in subjects with gunshots during World War I. In a seminal study in the British Journal of Ophthalmology, Holmes studied the effects of gunshot lesions in the occipital cortex and described the blind regions and visual disturbances and how these deficits depended and mapped onto the specific brain regions that were damaged (Holmes, 1918) **(Figure 5.2)**.

5.5. Neurophysiology in primary visual cortex

The initial and paradigm-shifting strides towards describing the neurophysiological responses in primary visual cortex were done by Torsten Wiesel and David Hubel. It is said that, to some extent, the history of visual

neuroscience is the history of visual stimuli. Typically, before the Hubel-Wiesel era, investigators had attempted to examine the responses in primary visual cortex using highly sub-optimal stimuli such as diffuse light or the type of point sources used to elicit activity in the retina and LGN. By a combination of inspiration, perspiration and careful observation, Hubel and Wiesel realized that neurons in primary visual cortex responded most strongly when a bar of a particular orientation was presented within the neuron's receptive field (Hubel and Wiesel, 1998). They went on to characterize the properties of V1 neurons in terms of their topography, orientation preference, ocular preference, color and so on. Their Nobel-prize winning discovery inspired generations of neurophysiologists to examine neuronal responses throughout the visual cortex.

There are probably more papers examining the neurophysiology of primary visual cortex than the rest of the visual cortex combined. A typical experiment often starts with determining the receptive field location of the neuron or neurons under study. In addition to single cell recordings, there has been increased interest recently in the use of multi-electrode arrays that can interrogate the activity of multiple neurons simultaneously. After determining the location of the receptive field, a battery of stimuli is used to probe the response preferences. These stimuli typically include either static or moving bars or gratings of different spatial frequencies and orientation.

A typical pattern of responses obtained from V1 recordings is illustrated in **Figure 5.3**. In this experiment, an oriented bar was moved within the receptive field. The direction of movement was perpendicular to the bar's orientation. Different orientations elicited drastically distinct numbers of action potentials in the response[3].

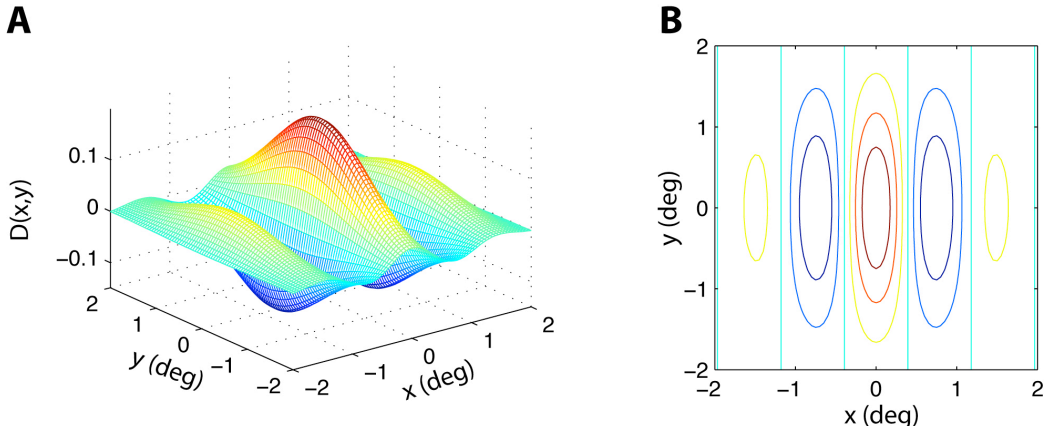
Another important aspect of neocortical circuits was discovered by Hubel and Wiesel by comparing the preferences of different neurons recorded during the same penetration. Advancing the electrode in a direction approximately tangential to the cortical surface, they discovered that different neurons along a penetration shared similar orientation preferences. This observation led to the notion of a *columnar structure*: neurons within a column have similar preferences, neurons in adjacent columns show a continuous variation in their preferences.

5.6. Quantitative description of the responses in primary visual cortex

[3] While the number of action potentials (or spike count) is not the only variable that can be used to define the neuronal response, it provides a simple and good starting point to examine neuronal preferences. For more details about neural coding, see Kreiman, G. (2004). Neural coding: computational and biophysical perspectives. Physics of Life Reviews *1*, 71-102.

220

Figure 5.4: The spatial structure of receptive fields of V1 neurons is often described by a Gabor function.



221 The receptive field structure of orientation-tuned simple V1 cells is often
222 mathematically characterized by a Gabor function. A Gabor function is the
223 product of an exponential and a cosine:
224
225

$$D(x,y) = \frac{1}{2\pi\sigma_x\sigma_y}\exp\left[-\frac{x^2}{2\sigma_x^2}-\frac{y^2}{2\sigma_y^2}\right]\cos(kx+\phi)$$

226
227

228 where σ_x and σ_y control the spatial spread of the receptive field, k controls the
229 spatial frequency and ϕ the phase (Dayan and Abbott, 2001). An example
230 illustration of a Gabor function is shown in **Figure 5.4**. The Gabor function is
231 characterized by an excitatory region as well as a surrounding inhibitory region.
232
233 In addition to the spatial aspects of the receptive field, it is important to
234 characterize the temporal dynamics of responses in V1. To a reasonable first
235 approximation, the spatial and temporal aspects of the receptive fields in V1 can
236 be considered to be independent or separable. The temporal aspects of the
237 receptive field can be described by the following equation:
238 $D(\tau) = \alpha exp(-\alpha\tau)\left[(\alpha\tau)^5/5! - (\alpha\tau)^7/7!\right]$
239 for τ >=0 and 0 otherwise.
240

241 ## 5.7. A simple model or orientation selectivity in primary visual cortex
242
243 In addition to recording neurophysiological activity, Hubel and Wiesel
244 proposed a simple and elegant biophysically plausible model of how orientation
245 tuning could arise form the responses of LGN-type receptive fields. In their
246 model, multiple LGN neurons with circularly symmetric center-surround receptive
247 fields oriented along a line were made to project and converge onto a single V1
248 neuron. Subsequent work gave rise to a plethora of other possible models and
249 there is still ongoing debate about the extent to which the Hubel-Wiesel purely
250 feed-forward model represents the only mechanism giving rise to orientation
251 selectivity in area V1 (e.g. (Carandini et al., 2005)). Still, this simple and elegant

interpretation of the origin of V1 receptive fields constitutes a remarkable example of how experimentalists can provide reasonable and profound models that account for their data. Furthermore, the basic ideas behind this model have been extended to explain the build-up of more complex neuronal preferences in other areas (e.g. (Serre et al., 2007)).

5.8. Simple and complex cells

A distinction is often made between "simple" and "complex" V1 neurons. The latter are less sensitive to the spatial frequency of the stimulus. Simple and complex cells are often distinguished by the ratio of the "DC" maintained response to their "AC" response elicited by a moving grating (De Valois et al., 1982). Complex cells show a small AC/DC ratio (typically <10) whereas simple cells have a larger AC/DC ratio (typically >10). In other words, complex cells show a higher degree of *tolerance* to the exact position of a bar with the preferred orientation within the receptive field. As we will discuss later, the alternation of visual selectivity changes from the previous stage in simple cells and the subsequent increase in tolerance at the level of complex cells has inspired the development of hierarchical computational models of object recognition.

Extending their model for orientation selectivity in simple cells by combining the output of LGN cells, Hubel and Wiesel proposed that the responses of a complex cells could originate by the combination of responses from multiple simple cells with similar orientation preferences but slightly shifted receptive fields.

Some complex cells also show "end-stopping", meaning that their optimum stimulus includes an end within the receptive field (as opposed to very long bars that end outside of the receptive field).

In spite of significant amounts of work investigating the neuronal properties in primary visual cortex, investigators do not agree in terms of how much still remains to be explained (Carandini et al., 2005). Biases in the recording procedures, stimuli, theories and ignorance of contextual effects and internal expectations may have an effect on the responses of neurons in V1. Yet, there has been significant progress over the last several years. Deciphering the neuronal preferences along the human ventral visual cortex is arguably one of the greatest adventures of Neuroscience.

References

Adrian, E. (1926). The impulses produced by sensory nerve endings. Part 2: The response of a single end-organ. Journal of Physiology *61,* 151-171.

Brodmann, K. (1909). Vergleichende Lokalisationslehre der Grosshirnnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues (Leipzig: Barth).

Carandini, M., Demb, J.B., Mante, V., Tolhurst, D.J., Dan, Y., Olshausen, B.A., Gallant, J.L., and Rust, N.C. (2005). Do we know what the early visual system does? J Neurosci *25*, 10577-10597.

Dayan, P., and Abbott, L. (2001). Theoretical Neuroscience (Cambridge: MIT Press).

De Valois, R.L., Albrecht, D.G., and Thorell, L.G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. Vision Res *22*, 545-559.

Felleman, D.J., and Van Essen, D.C. (1991). Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex *1*, 1-47.

Finger, S. (2000). Minds behind the brain. A history of the pioneers and their discoveries. (New York: Oxford University Press).

Holmes, G. (1918). Disturbances of vision by cerebral lesions. British Journal of Ophthalmology *2*, 353-384.

Hubel, D.H., and Wiesel, T.N. (1998). Early exploration of the visual cortex. Neuron *20*, 401-412.

Kandel, E., Schwartz, J., and Jessell, T. (2000). Principles of Neural Science, 4th edn (New York: McGraw-Hill).

Kreiman, G. (2004). Neural coding: computational and biophysical perspectives. Physics of Life Reviews *1*, 71-102.

Serre, T., Kreiman, G., Kouh, M., Cadieu, C., Knoblich, U., and Poggio, T. (2007). A quantitative theory of immediate visual recognition. Progress In Brain Research *165C*, 33-56.