

**BEWARE: These are preliminary notes. In the future, they will become part of a textbook on Visual Object Recognition.**

## Chapter 5: 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<sup>1</sup>. Primary visual cortex is the first stage where information from the two eyes converges onto individual neurons.

### 3.1 About neocortex

The human neocortex is about 2-4 mm thick; it is characterized by multiple convolutions such that it can fit about 2600 cm<sup>2</sup>. Brodmann subdivided neocortex into multiple areas based on morphological and anatomical considerations as shown in **Figure 3.1** (Brodmann, 1909). Subsequent physiological and lesion studies have shown that many of these structural subdivisions correlate with clear functional differences. Localization of brain function has a long and rich history that continues to current days (Finger, 2000).

Primary visual cortex has a stereotypical architecture that is, to a coarse approximation, similar to other parts of visual neocortex. The neocortical sheet is characterized by six layers that show a stereotypic connectivity pattern. With exceptions (it is biology after all), this canonical connectivity pattern is shared across different visual areas and also across different sensory modalities. Layer 1 is the most superficial layer and contains few cell bodies. 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. In contrast, top-down connections typically end in the deep layers 5 and 6 (Felleman and Van Essen, 1991). 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.

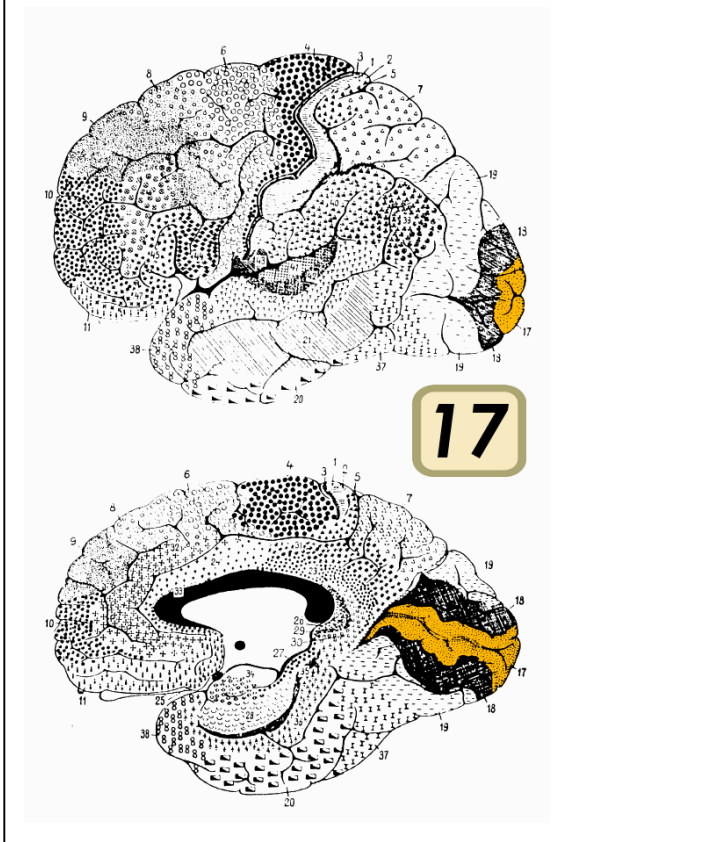
### 3.2 How to study neuronal circuits

Every problem has an appropriate scale that is particularly appropriate. For example, it is particularly tedious and difficult to attempt to read the newspaper using a microscope or from a distance of 20 meters away. In the

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<sup>1</sup> In the cat literature, primary visual cortex is also referred to as area 17.

**Figure 3.1: 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].**



case of neocortical circuits, this 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)<sup>2</sup> 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 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

<sup>2</sup> A few neurons only show graded voltage responses and do not emit action potentials.

Figure 3.2: Visual deficits obtained from gunshots as mapped by Holmes [source=British Journal of Ophthalmology (1918) 2:353-384].

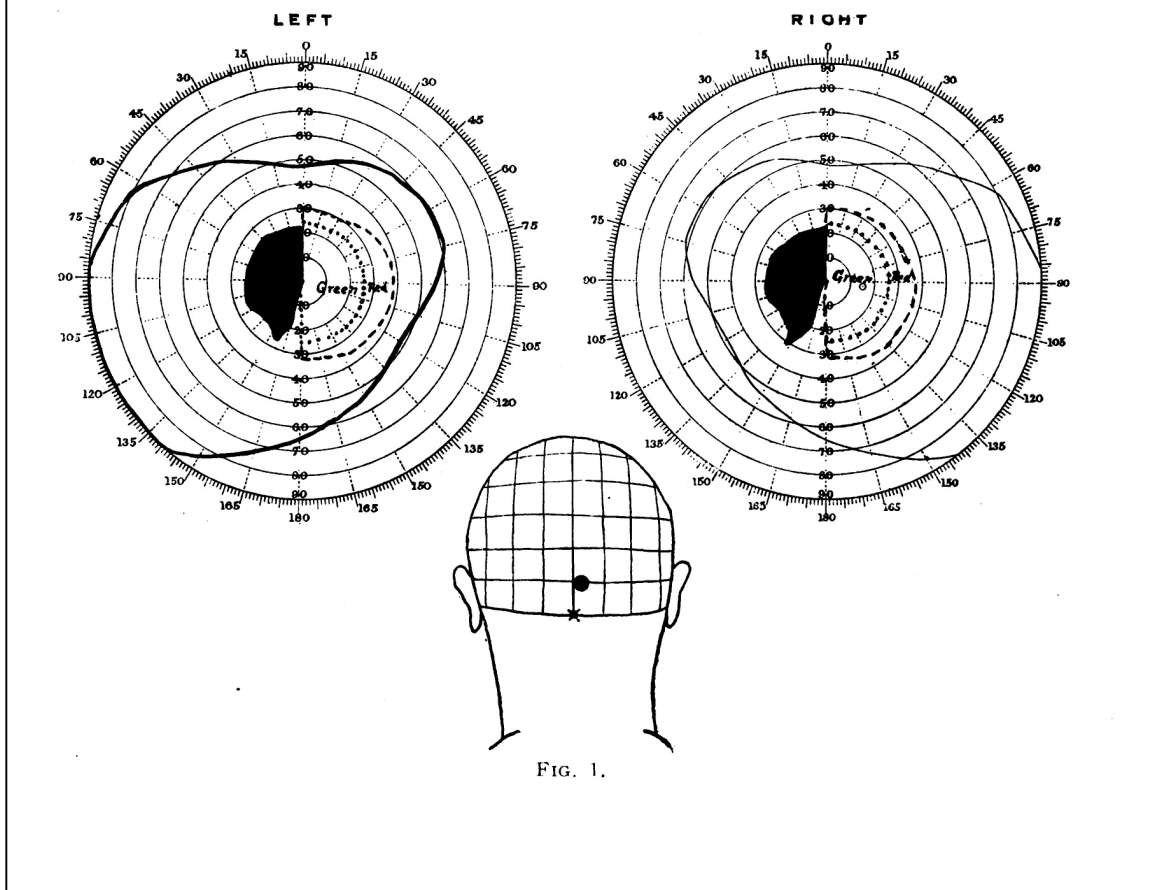


FIG. 1.

individual neurons. The methodology was established by Edgar Adrian (Adrian, 1926).

### 3.2 Nearby neurons show similar properties

The primary visual cortex is about 2 mm thick and the entire surface is a few square inches. 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

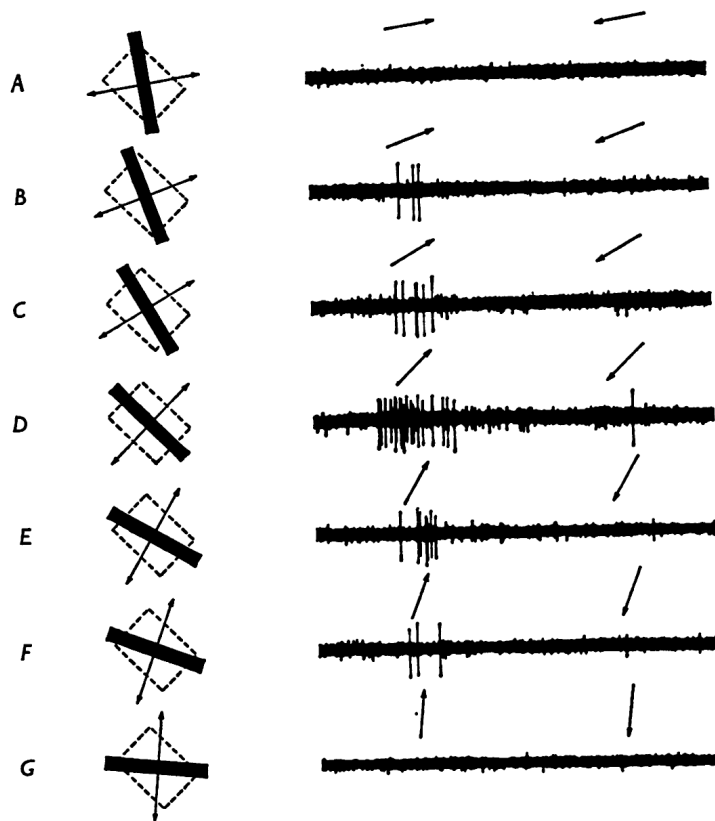
retinotopically organized, meaning that nearby neurons have receptive fields that map onto nearby parts of the visual field and of the retina.

### 3.3 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 3.2).

Figure 3.3: 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]



### 3.4

#### 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.

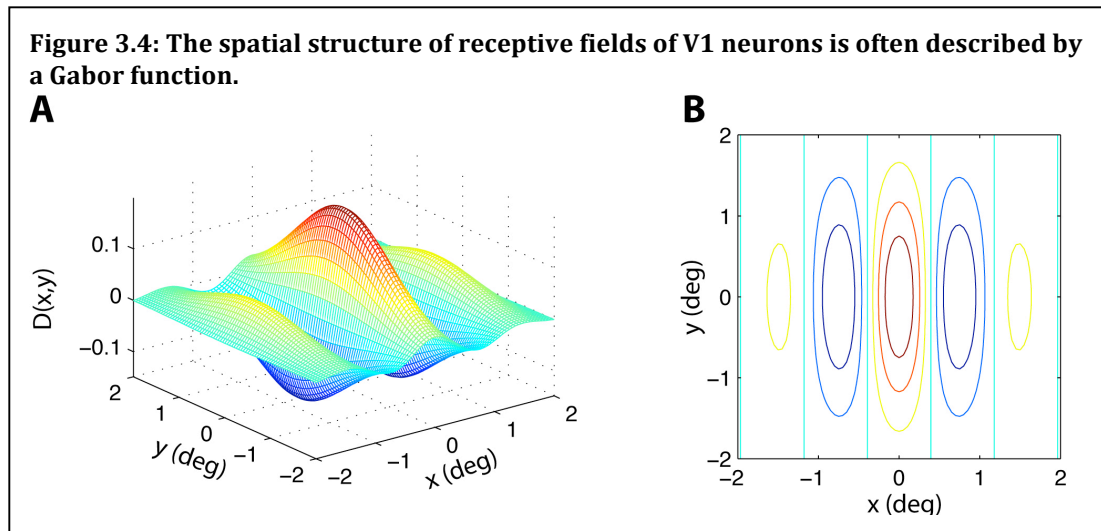
A typical pattern of responses obtained from V1 recordings is illustrated in **Figure 3.3**. In this experiment, an oriented bar was moved within the receptive field. The direction of movement was perpendicular to the bar's orientation. Different orientations elicited drastically distinct numbers of action potentials in the response<sup>3</sup>.

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.

### 3.5 Quantitative description of the responses in primary visual cortex

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<sup>3</sup> 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.



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

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

where  $\sigma_x$  and  $\sigma_y$  control the spatial spread of the receptive field,  $k$  controls the spatial frequency and  $\phi$  the phase (Dayan and Abbott, 2001). An example illustration of a Gabor function is shown in Figure 3.4. The Gabor function is characterized by an excitatory region as well as a surrounding inhibitory region.

In addition to the spatial aspects of the receptive field, it is important to characterize the temporal dynamics of responses in V1. To a reasonable first approximation, the spatial and temporal aspects of the receptive fields in V1 can be considered to be independent or separable. The temporal aspects of the receptive field can be described by the following equation:

$$D(\tau) = \alpha \exp(-\alpha\tau) \left[ (\alpha\tau)^5 / 5! - (\alpha\tau)^7 / 7! \right]$$

for  $\tau \geq 0$  and 0 otherwise.

### 3.6 A simple model of orientation selectivity in primary visual cortex

In addition to recording neurophysiological activity, Hubel and Wiesel proposed a simple and elegant biophysically plausible model of how orientation tuning could arise from the responses of LGN-type receptive fields. In their model, multiple LGN neurons with circularly symmetric center-surround receptive fields oriented along a line were made to project and converge onto a single V1 neuron. Subsequent work gave rise to a plethora of other possible models and there is still ongoing debate about the extent to which the Hubel-Wiesel purely feed-forward model represents the only mechanism giving rise to orientation 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)).

### 3.7 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.

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