In the preceding lectures we discussed the tuning properties of a population of neurons and calculated using Fisher information how well we could estimate the stimulus properties based on the firing rate responses of these neurons. Furthermore, we developed methods to calculate entropy and mutual information that could be used to estimate how much information is represented in the (temporal dynamics of) spike trains. These neurons are located somewhere in the cortex. In the following lecture I will discuss some general principles to build cortical maps, which tell where neurons with a particular feature preference are located. I will do this using the visual system as an example to which I will give a brief introduction for the physicists in the class.

The visual pathway, illustrated in Figure 1, starts with photons hitting the retina, which turns these into action potentials, which are transmitted across the optic tract to the thalamus (lateral geniculate nucleus – LGN). From the thalamus it goes to the primary visual cortex, and from there on it gets somewhat complicated. Figure 2, taken from a classic 1991 paper by Felleman and Van Essen, shows in color the cortical areas in the macaque involved in vision (Felleman & Van Essen, 1991). The top and bottom left part show the areas on the cortical surface, whereas the right panel shows an unfolded (flat) map of the cortex. In classic experiments performed by Hubel and Wiesel in cat and macaque primary visual cortex it was found that the cells there were orientation selective (Hubel & Wiesel, 1968). The cells in retina and thalamus have a circular receptive field (RF) with center-surround organization, which means they respond to a light spot at the center of the RF with an increase in firing rate, whereas the same spot a bit off center will cause a decrease in firing rate. (Note that the cells fire at a low, but nonzero rate, when there is no visual stimulation). Hubel & Wiesel therefore tried to stimulate V1 cells they recorded from with light spots, but were
initially unsuccessful. Only when by accident they pulled out the slide from the slide-projector used to present the stimulus, the cell they were recording from started spiking. When they then varied the orientation of the line, they found that the cell responded most to one orientation, with the firing rate looking like a bell-curve as a function of orientation. This is the basis for the tuning functions we used in the lecture about Fisher information. Before going into more detail, we will discuss what happens in "higher" cortical areas. The different areas shown in Figure 2 are connected in a network, for which a hierarchy can be defined. This network was constructed by Felleman & Van Essen using a large number of anatomical studies, and is shown in Figure 3. The cortex has a laminar structure, with feedforward connections often leaving from the superficial (supragranular, L2/3) layers and ending in the granular layer (L4), whereas feedback projection have another profile. Hence, by determining where projections start and end, feedforward can be distinguished from feedback, thereby leading to the diagram shown. This diagram is not the end-all be-all. For instance, when brief light flashes were presented, visual cortical areas respond at different latencies. In these tests the frontal eye field (FEF) responded before area V4, even though in the diagram FEF comes later than V4 (Schmolesky et al., 1998).

Cells in area V1 are orientation selective, whereas those in LGN and the retina are not. This means that a new property has emerged because of the specific form of the feedforward circuitry as well as recurrent connections within V1 itself. What properties are added in higher visual areas? A tentative answer to this question can be given by considering invasive recordings in human volunteers. In some patients epilepsy cannot be controlled through pharmacological therapies, which means that part of the brain will need to be removed in order to give the patient quality of life. As part of this procedure electrodes are implanted in patients to pinpoint the part of the brain where the seizures originate and to make sure that no important parts are removed. In the course of this evaluation patients can volunteer to be part of an experimental study. In the study shown in Figure 4, the patients were shown images of famous people and objects, while single cell activity was recorded in locations near the hippocampus and temporal lobe (Quiroga et al., 2005). In each panel, from top to bottom, the image, the spike rasters and the spike time histogram is shown. The panels that are highlighted all show Jennifer Anniston in various poses. This suggests that this neuron can recognize Jennifer Anniston. Interestingly, it does not respond that much when Brad Pitt is also present in the picture. Neurons responding to Bill Clinton, Halle Berry etc were also observed. It is not the case that this neuron alone is
responsible for this recognition, as it is part of a large network. Nevertheless it shows that a single neuron can integrate a large number of tuned synaptic inputs into a quite specifically tuned response.

Neurons in V1 have a receptive field, this is the area to which the neuron responds to a visual stimulus by either increasing or decreasing its firing rate. Sometimes, the concept of minimal response field is used, this is the range in which a small stimulus by itself will elicit a response. The firing rate within the receptive field is given by a tuning function

$$ R(\theta_s | \theta_p) = R_0 + (R_{\text{max}} - R_0) \exp \left( -\frac{(\theta_s - \theta_p)^2}{2\sigma^2} \right) $$

Here there are two angles, the one labeled by s stands for the stimulus orientation, whereas the one labeled p stands for the preferred orientation of the neuron. $R_0$ is the spontaneous firing rate and $R_{\text{max}}$ is the maximal rate, which is obtained when the stimulus orientation matches the preferred orientation. The latter depends on the contrast of the stimulus, but this dependence is omitted for simplicity. The neuron is not only labeled by the preferred orientation, but also by the location of the receptive field center in the visual field, say $x_r$ and $y_r$ (in degrees of visual field). There could be other tuning properties such as spatial frequency, color, ocular dominance etc. All these tuning properties depend on the location of the neuron on the cortex, say $x_c$ and $y_c$ (in millimeters, mm), which defines a cortical map for each property.

The cortical map is constrained by physical principles. To obtain a particular tuning property, a specific feed forward and recurrent connectivity is required, which implies a wiring, from axons to dendrites of the postsynaptic neuron. This wiring takes up space and needs to be efficient to keep the size of the brain reasonable (for instance from a metabolic perspective). **Key principle:** tuning properties are arranged to minimize wire length. As a consequence self-organized maps emerge, with (in primates, cats) cortical minicolumns, roughly 30 microns in diameter, comprised of neurons with similar tuning properties.
The RF center map can be determined as follows. A strong stimulus (Figure 5) that strongly activates neurons at particular locations is presented for a long duration while radioactive glucose is present in the blood. The cells that are activated need more energy than the non-activated ones, and thus take up more glucose. When the brain is placed on photographic paper, the radioactive decay labels the location of the most active neurons (Tootell et al., 1988).

**Self-test 1.** Why is this a good stimulus? In your explanation discuss the “checkerboard” appearance.

The resulting response is shown in Figure 6. The radial spokes and circles are mapped into Cartesian coordinates, i.e. perpendicularly intersecting lines. The circle sectors are mapped into squares. The visual field is described by an angle denoted by \( \theta \) and an eccentricity, which is the radial distance, and is denoted by \( r \). This is mapped into \( x \) and \( y \) coordinates in the cortex using

\[
(r, \theta) \rightarrow (x, y) = \left( \log\left(1 + \frac{r}{r_0}\right), -\frac{r \theta}{r_0}\right)
\]

This means that circles are mapped to vertical lines and circle-sectors to horizontal lines as indicated in figure 7.

**Self-test 2.** The same procedure gave rise to a checkerboard activation pattern on the cortex. What was the stimulus? (See Figure 8).

A few years later scientists discovered the method of intrinsic imaging. As students in of research master cognitive neuroscience may know, the fMRI signal is generated by the blood oxygen dependent level (BOLD) signal, which represents metabolic activity. Intrinsic imaging uses the same signal, so that the level of activity on a time scale of seconds can be measured in the cortex, with active spots showing up dark. This method was used to determine orientation maps. Gratings of different orientations (Figure 9) were presented for a few seconds and the response was
measured. To enhance the signal to noise ratio, these experiments were done in pairs: the response to the orthogonal orientation was subtracted, such that a set of dark areas (activated by the first stimulus) and white areas (activated by the orthogonal stimulus) appeared, this is shown in Figure 10. For each pixel, the activation for a number of different orientations are available, a map is created by picking the orientation that led to the strongest activation as the pixel’s preferred orientation and color coding that orientation (Figure 11). The resulting map shows variation on the mm scale, which means that neurons within an area of less than 1mm² can represent roughly all orientations. This is called a hypercolumn.

We can distinguish a number of features of this map (Figure 12).

- There are distortions, it is not a regular map, with, say, squares preferring the same orientation.
- There are so called linear zones, where the preferred orientation varies linearly with distance on the cortical surface.
- There are fractures, lines across which the preferred orientation varies abruptly.
- There are singularities, when you go around such a singular point, you will encounter all the orientations.
- There are saddle points, where the preferred orientation approaches a certain value and then turns away from it, returning in the same way (i.e. sequence of orientations).
- There is a relation between ocular dominance, which eye a neuron/pixel responds to most strongest, and the orientation tuning map.

Self-organizing maps (SOM), also referred to as Kohonen maps can reproduce salient features of orientation maps (Obermayer et al., 1992). SOMs are used to map from feature space to cortical space. The key problem is that there are more features (at least 3: orientation and 2D RF position) than there is space to map on, which is the two-dimensional cortex. SOMs solve this by reserving for each element of “feature-space” volume about the same amount of cortical area. To see this imagine a crumpled sheet of paper: it lives in 3D space, but you can “walk” across it in 2D. The key principle is that nearby feature values should be mapped to nearby points on the cortex, which should also reduce wire-length.

To set the stage we discuss a simpler problem, representing a 2D square on a 1D cortex, because it is easier to visualize. What we want is a map from 1D to 2D, \((x(c), y(c))\). Here \(c\) labels the position on the 1D cortex, and \((x, y)\) is the position in
feature space in the square. This whole function can be plotted as curved line in the 2D square. What we have to achieve is to minimize the length of this curve in feature space, because then nearby points in cortex represent nearby points in feature space.

First, we need to choose how many points to use to represent the cortex, this is the variable \( M = 50 \). Then we need to decide how big feature space is, here we choose to represent a 5 by 5 square. The algorithm starts by randomly assigning positions to each of the \( M \) different \( c \). We either put them on a line or spread them out randomly across the square (Figure 13, left and right).

The map is then iteratively improved. A random feature vector is generated. This feature vector should be represented by a nearby point on the map. This is in general not the case, due to our initial condition. To improve the map, the nearest point on the map is moved closer to the random feature vector. To ensure that the length of the cortical line is small, points in the neighborhood also have to move with this closest point. There are two corresponding parameters in the algorithm, “eps” how much to move, and “sigma” which is the size of the neighborhood – in cortical coordinates on the line – that moves with the closest point. This neighborhood is defined as a Gaussian multiplicative factor with the closest point as center and sigma as standard deviation. These adjustments are done for many randomly generated points that uniformly fill feature space.

**Self-test 3.** Write a schematic program that achieves these moves. (You will do this in more detail during the practice hours).

In Figure 14, we show a few graphs as the simulation progresses. Each iteration is comprised of 50 adjustments. You can see that initially it still looks very diagonal, but gets pulled out in the perpendicular direction (iterations 3, 10, 50) by feature vectors uniformly distributed in the square. In the last panel shown, iteration 100, the curve fills space.
Self-test 4. What do you think the figure will look like for M=500? You can test your prediction during the practice hour.

For your pleasure I include some pretty graphs of orientation/position maps produced by the Kohonen algorithm used to map 4D (2D space, 2D for orientation) to 2D.

References


