In part 1 we discussed Kohonen maps and said that they embodied in some sense the minimal wire length solution. Koualakov & Chklovskii have investigated directly what type of orientation maps would emerge by wire length minimalization (Koulakov & Chklovskii, 2001). Their goal was to find out whether so called pinwheels, singularities in the orientation map observed experimentally, would emerge naturally as a consequence of wire-length considerations. Earlier it was shown by mathematical analysis of the Hamiltonian

\[ H = \int d\bar{r}d\bar{r}' J(|\bar{r} - \bar{r}'|)\cos(\theta(\bar{r}') - \theta(\bar{r})) \]

that the optimal map, \( \theta(\bar{r}) \), had a so called ice cube form (see below). They considered a cortex of dimensions \( N \) by \( N \), each with a preferred orientation (PO), and whose connectivity was described by a binary connection matrix of \( N^2 \) by \( N^2 \). They constrained connections by requiring that a fraction \( c(\Delta\theta) \) of the connections came from neurons with a PO that differed by \( \Delta\theta \). This restricts the distribution of inputs, but does not constrain the distribution of outputs. They optimized \( \theta(\bar{r}) \) as follows. They started with a random initial setting for the map, and for each location they looked (more details are in the original paper (Koulakov & Chklovskii, 2001)) for all neurons with orientations that were different by \( \Delta\theta \) and picked the number of neurons required by \( c(\Delta\theta) \) that were closest in distance, this was done for all differences and for all neurons. For this minimal wire-length configuration, the wire length was determined. The map was then iteratively modified, by picking a location, changing the PO at that location, redoing the previous procedure to minimize wire length and then accepting the new PO if it reduced wire length, or accepting at a probability according to the Metropolis Monte Carlo scheme when it increased wire length (this is to get out of local minima). The size of the change in PO was adjusted so that less than 30% of the changes were rejected. They parameterized \( c(\Delta\theta) \) by three parameters:

\[ c(\Delta\theta) = c_{90} + (c_0 - c_{90})\exp(-\Delta\theta^2/2a^2) \]

Figure 16. (A,B) Salt and pepper; (C,D icecube and (E,F) wavy ice cube configurations
The width parameter \(a\), and the background (uniform) probability \(c_{90}\) and the peak height \(c_0\).

Figure 16 shows the obtained maps for different settings of these parameters. The resulting maps are a competition between two processes. First, when the connection probability is flat, you want all orientations to be nearby, which leads to a salt and pepper organization (Figure 16, panels A, B). Second, when the connection probability is peaked, neurons with similar PO should be nearby, which leads to a ice cube (panels C & D), in which the same PO are organized in columns, or for sharper \(c(\Delta \theta)\) so called wavy ice cubes (panels E & F). In Figure 17, the combination of a sharp peak and a strong uniform background is studied. In panels A-C, the first case is shown, in which an array of pinwheels is visible. This may be hard to see, which is why the authors show a map of the gradient in the phase across the cortical surface, wherein hot-spots indicate steep changes in phase that correspond to pinwheels. For another parameter setting, shown in panels E-G, there are not only pinwheels but also fractures, indicated by the lines in the gradient map.

**Self-test 5.** What is missing in this analysis and how would that change the results?

Feature maps are a powerful concept to explain population responses in the visual cortex. How many of them are there and how do they interact? In the following we discuss two papers concerned with these issues. The first is by Basole and coworkers and argues there is only one map (Basole et al., 2003), whereas the second extracts the consequences of a bias in the position map in the ferret for other feature maps.
There is a difference between direction of motion and orientation. A drifting horizontal grating has an orientation of 0 degrees and has a direction of motion in the vertical direction, at 90 degrees, hence perpendicular to it. Such a stimulus activates cells that we say prefer an orientation of 0 degrees. In a grating the direction of motion is always perpendicular to the orientation so one cannot investigate whether there are separate maps for these properties. Short rectangular bars can have direction of motion that is not perpendicular to the orientation. The question is, will such a stimulus activate cells corresponding to the orientation of the bar, or corresponding to the direction of motion, or a completely different set of cells. This was studied by Amit Basole and the results are shown in Figure 17bis. In the panel A, the activation map, obtained through intrinsic imaging, is shown, with on top a schematic representation of the stimulus and at the bottom a close up of the activation map. In the left-most panel A, the response to bars and in the middle panel B the response to gratings is shown. On the right, panel C, the population response profile (PRP) is shown. In it, the mean activation for each set of pixels with the same PO is plotted as a function of PO. The peak of this curve indicates the “perceived” orientation. The first example, that is panels A to C, the bars have a consistent direction of motion, i.e. perpendicular to their orientation. The areas activated in cortex are the same as for a regular grating with the same orientation. Which is exemplified in panel C by the overlap between the gray and black curves. When the same orientated bars move in the vertical direction (D-F), the motion signal would indicate an orientation of zero degrees and the orientation of the bars itself would indicate 45 degrees. The areas activated by stimulus look most like those activated by a grating of 22 degrees. This means that the orientation has been shifted closer to that corresponding to the motion signal. In the last example (G-H), the motion is in the horizontal direction (corresponding orientation=90 degrees), hence the population response shifts from 45 degrees in the direction of 90 degrees, ending up at 75 degrees.

This shows that there is competition between the two orientation-indicating signals. When the bars are longer, the orientation signal should be stronger, whereas when the bars are moving faster you would expect the motion signal to be stronger. The former is illustrated in figure 18. There 45 degree bars are moving in the horizontal direction (90 degree orientation), and their length is varied. For short length, the peak of the PRP is near 90 degree whereas for long stimuli is near 45 degrees, as expected.
**Self-test 6.** In Figure 19, the same paradigm is shown, but now the velocity is varied. Can you explain the peak shift from 73 degrees (low speed) to 17 degrees (high speed).

These results can be explained by the existence of neurons tuned for spatiotemporal energy, this means neurons that respond mostly to energy at a particular combination of k vector (spatial frequency) and ω (temporal frequency). Hence, drifting gratings correspond to a point in (k, ω) space, and precisely activate particular cells. By Fourier transforming the moving grid of rectangular bars, one can determine the PO of the cells whose (k, ω) preference overlaps best with that of the stimulus. This then gives the perceived orientation. This somewhat involved calculation is performed in Mante et al (Mante & Carandini, 2003; 2005).

Kohonen maps generate orientation maps that look similar to experimentally measured maps, but can we derive other predictions from them? Yu et al. performed intrinsic imaging experiments on Ferret primary visual cortex (Yu *et al.*, 2005). The cortical magnification factor indicates how much space in cortex is needed to represent a distance in real space (in terms of RF centers). The magnification factor for elevation is 4 times higher than for azimuth, this means that the distance on the cortical surface between equi-elevation lines is larger than the distance between equi-azimuth.

Figure 20 the results of simulations of such an anisotropic models are shown (panel A) and compared to an isotropic cortex (panel D). The iso-elevation lines are horizontal and the iso-azimuth are vertical. The Kohonen model not only represented two-dimensional RF position but also orientation (color code in A and D) and ocular dominance (B and E). It turns out that the anisotropy in space, causes anisotropy in orientation, spatial frequency and ocular dominance, the corresponding gradients are perpendicular to those in position (retinotopic) space. This is quantified in terms of the histograms of the intersection angle between gradients of (black) orientation,
(blue) ocular dominance and (red) spatial frequency with retinotopic gradient (Panels C and F). In Figure 21 is the corresponding anisotropy in experimental results shown, orientation+retinotopic map. In Figure 22 the intersection angles are shown, B: orientation, C: ocular dominance and D: spatial frequency. The blue curves are for the pixels with gradients in the 30th percentile. These match the theoretical results. Consult the original paper for details (Yu et al., 2005).

References


