Intracortical mechanism of stimulus-timing-dependent plasticity in visual cortical orientation tuning

This paper describes how a cortical hebbian learning rule bases on spike-timing dependent plasticity can account for changes in the orientation tuning of cortical pyramidal cells.

Reminders:

1) Visual stimuli from the retina are transmitted to visual cortex area V1 (primary visual cortex) via the lateral geniculate nucleus (LGN, in the thalamus).

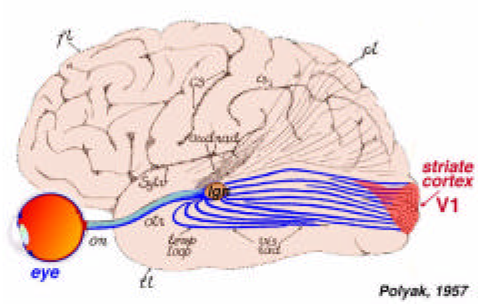


Figure 8. Visual input to the brain goes from eye to LGN and then to primary visual cortex, or area V1, which is located in the posterior of the occipital lobe. Adapted from Polyak (1957).

from http://webvision.med.utah.edu

2) Pyramidal cells in area V1 receive inputs from either the left or right visual field only. Cells responsive to the left of right visual field alternate in V1, creating the so-called “ocular dominance columns”.

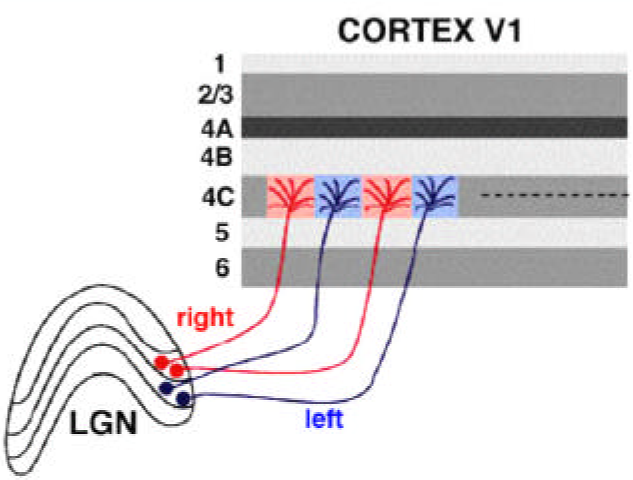


Figure 14. The signals from each eye are segregated within the LGN and go into different ocular dominance columns within area V1, layer 4C.

from http://webvision.med.utah.edu

3) The signals in area V1 are also retinotopically arranged. Thus the striate cortex retains the retinotopic map of the contralateral visual fie ld that is developed in the LGN.

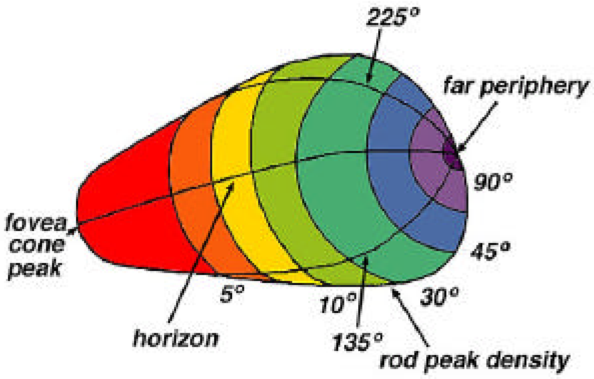


Figure 20. The unfolded striate cortex has a shape like a pear. It would be a quarter sphere if the visual fields were equally represented everywhere, but instead it is greatly distorted by the disproportionate representation of parts near the center of gaze (fovea), a feature termed "cortical magnification". In contrast, the far periphery is greatly underrepresented.

4) V1 is the first site where strong orientation and direction selectivities are observed in the macaque monkey. While the vast majority of V1 cells show some degree of orientation selectivity, only approximately 25-35% of V1 cells are strongly directionally selective. The classic method for testing orientation and direction selectivity is to measure the spike rate of a single cell in response to drifting oriented luminance bars and/or drifting luminance spots.

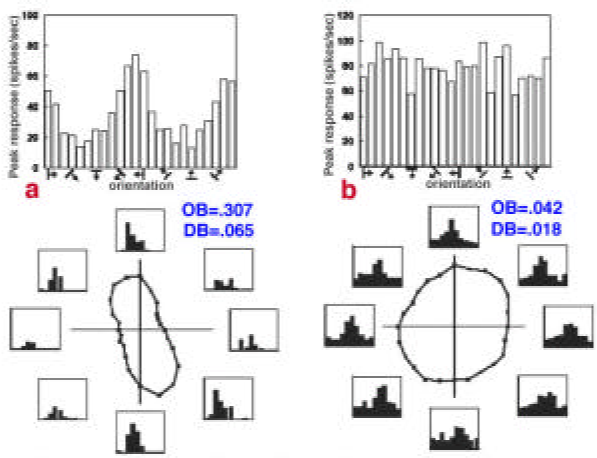
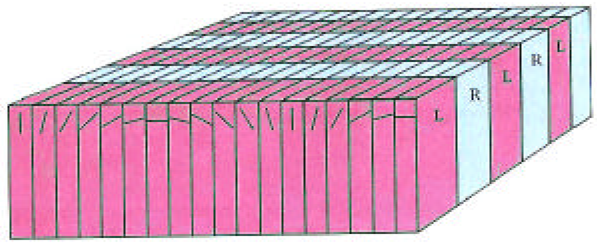


Figure 21. A tuning curve and corresponding polar plot obtained from two macaque V1 cells in response to drifting luminance bars of systematically varied orientation and direction. The responses of one orientation selective cell and one nonselective cell are provided for comparison. Histograms surrounding the polar plots demonstrate the cellular response as a function of time. Orientation bias (OB) and direction bias (DB) are measures of how selective a cell is, where >0.1 is significant, and 0.3 is approximately an 8:1 maximum firing rate to minimum firing rate ratio. From Schmolesky et al. (2000).

5) Orientation and ocular dominance columns are thought to define the functional organization of primary visual cortex.



Orientation and ocular dominance columns

Figure 23. The ice-cube model of the cortex. It illustrates how the cortex is divided, at the same time, into two kinds of slabs, one set of ocular dominance (left and right) and one set for orientation. The model should not be taken literally: Neither set is as regular as this, and the orientation slabs especially are far from parallel or straight.

Results

1) <u>Interocular transfer in electrophysiological experiments</u>

Only cells which had clear orientation tuning in response to stimulation of both eyes were used in this study.

Cells were then conditioned by presenting repeated sequences of their optimal stimulus and a closely related, non-optimal stimulus.

1) Measure orientation selectivity of cell in response to stimulation of each eye. This results in An orientation tuning curve for each cell with an optimal orientation S_0.

2) Then "condition" the cell by repeatedly presenting two stimuli at 8.2 ms intervals. Two conditioning paradigms were used:
A) $S_0 - S_{+/-15}$ separated by 8.2 ms
B) $S_{+/-15} - S_0$ separated by 8.2 ms.

3) After the conditioning phase, the orientation selectivity was measured again by presenting stimuli to the non-conditioned eye!

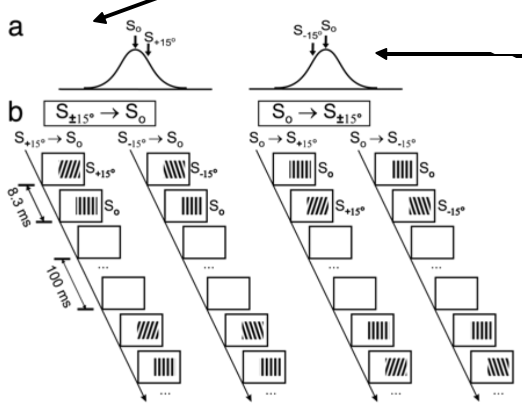
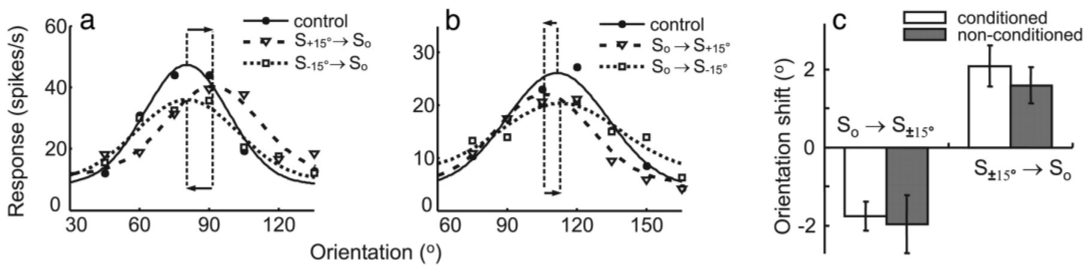


Fig. 1. Conditioning stimuli used to induce shift in orientation tuning. (*a*) Orientations of conditioning stimuli (arrows) relative to tuning (curve) of the cell. *S*o, optimal orientation; *S*+15° and *S*-15°, 15° clockwise and counterclockwise from optimal. (*b*) Four types of conditioning stimuli. For interocular transfer experiments, only *S*o and *S*±15° (according to tuning measured through the conditioned eye) were used. To measure orientation specificity of the effect (Fig. 6), other orientations were also used.

It was found that after $S_{+15^\circ}{}^{->}S_o$ conditioning, the optimal orientation through the non conditioned eye shifted toward S_{+15°, whereas S_{-15° -> S_o conditioning induced a shift toward S_{-15}.
Conditioning in the reverse order (S_o ->$S_{\pm15^\circ}$), on the contrary, induced a shift away from the non optimal conditioning orientation.



2) Intraocular transfer in psychophysics experiments

Human subjects were shown gratings with +7 or -7 degrees orientation from the vertical and had to judge if the grating was tilted clockwise or counter clockwise. They were conditioned by flashing of pairs of vertical or shifted gratings at 8.2 ms separated by 8.3 ms. After conditioning, subjects were tested again.

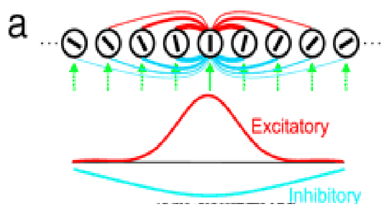
For all four subjects tested, S_{-7° -> S_{+7° monocular conditioning caused a shift in the perceived orientation through the nonconditioned eye toward S_{+7°, whereas S_{+7° -> S_{-7° conditioning induced an opposite shift.

3) Cortical spike timing

Duirng extracellular ecordings, the authors show that cells tend to respond with earlier spikes to their preferred orientation than to a shifted orientation. As a consequence, when the system is stimulated with a sequence of $S_{shifted}$-S_0, a given cell would receive inputs from cells who prefer $S_{shifted}$ before it responds to the stimulus itself.

4. Modeling

The authors then construct a model of orientation selective cells to test of differences in spike timing, in combination with a spike-timing-dependent plasticity rule can underlie the observed changes in orientation tuning and in psychophysical experiments.
The detailed equations are not very important. It is important to note that each neuron received both orientation-selective feedforward inputs (green arrows) and intracortical connections from other orientation columns (red and blue lines).
Cells are spiking, and the excitatory synapses between pyramidal cells undergo spike-timing dependent plasticity during the conditioning phase.
The equations describe the input each cell would receive in response to a stimulus of a given orientation.



$$\tau_0 \frac{\partial V_k(t)}{\partial t} + V_k(t) = V_k^{ff}(t) + \sum_{j=1}^{j=36} V_{k,j}^{\mathrm{rec}}(t),$$

$V_k(t)$: membrane voltage of pyramidal cell k.
To: membrane time constant
$V_k^{ff}(t)$: feedforward (afferent) input (green arrows)
$V_{k,j}^{rec}(t)$: recurrent input from other cells.

This equation describes how the membrane voltage evolves in time due to external inputs (leaky integrator).

Remember: τ dv/dt = -v + inputs

In response to a give stimulus orientation, each cell receives a combination of feedforward input, output of other Cells (narrowly tuned) and input of more braodly tuned cells.

It was found that $S_{+15°}$ -> S_o conditioning (interval 8.3 ms) induced a rightward shift in tuning of the model neuron preferring 0°, and S_o -> $S_{+15°}$ conditioning induced a leftward shift (dotted curve), consistent with the experimental finding.