

Chapter 5

Conclusions

The central theme of this thesis has been the role of the environment in the development and maintenance of selectivity. We introduced this concept in Chapter 1, and explored some simple low dimensional environments. In the one dimensional environment, using the BCM learning rule, it was shown that fairly complex oscillations result that depend on the internal parameters of the neuron, and also on the value of the input. This type of behavior could lead to an experimental determination of those internal parameters in a fairly straightforward fashion.

It was also shown that significant differences could be seen between models which may at first seem to be similar. This difference was explored more rigorously, in a much more realistic environment in Chapter 2. We continued our goal of comparison to experiment, using the deprivation protocols as a basis. It was found that a parameter regime could be obtained for BCM which was consistent with the rough dynamics of *all* the major deprivation experiments (monocular deprivation, binocular deprivation, and reverse suture). It was critical to have a *single* parameter set to be consistent with *all* the experiments, in order to confidently state that the model was truly consistent.

It was further found that the PCA rule had some inconsistencies with the timing of deprivation experiments. The most drastic of these is for binocular deprivation, where the PCA rule and any other correlation-based rule perform a random walk about the normal state, not significantly losing selectivity. Other problems with correlation-based rules were outlined in Chapter 2, leading to the conclusion that rules which depended only on second order statistics did not lead to consequences in agreement with experiment. One noteworthy observation from the PCA rule was the dependence on noise for the timing of the deprivation. It was found that, for PCA, the *more noise* into the closed eye for monocular deprivation, the *slower* the drop in response of the cell to the closed eye. This was the opposite behavior obtained for BCM, where *more noise* into the closed eye leads to a *faster* drop in response. This observation was the motivation for an experiment to determine which rule was consistent with nature.

In Chapter 3 we introduced other learning rules, which depended on higher order statistics.

These rules were derived from cost functions, using the projection pursuit formalism. It was shown that the noise dependence observed in Chapter 2 was not restricted to the PCA rule, but was a property of all rules investigated that had a strongly heterosynaptic stabilization mechanism. The experiment which was performed to measure this dependence (Rittenhouse et al., 1998) showed that the primarily homosynaptic rules led to predictions in agreement with observation.

A simple model of the input statistics was introduced in order to explore some of these properties. It was shown that the results of deprivation could be thought of as the competition between input distributions: structured input winning over unstructured input. It was also shown that BCM is sensitive to the sigmoid, or the interpretation of spontaneous activity, which is crucial to the proper working of binocular deprivation. More work has to be done to explore this sensitivity, in order to determine its origin and consequences.

Finally, a number of extensions were presented in Chapter 4. These included the role of X and Y retinal cells and the development of direction selectivity in the cortex. It demonstrated that some of the rules presented, including the BCM rule, are quite robust to changes in the preprocessing. It also shows how seemingly unrelated phenomena, such as ocular dominance and direction selectivity, could arise from the *same underlying mechanisms*. This gives new hope that the multitude of phenomena found in the brain could be understood from a few simple rules. From these examples it is easy to see how the model can be extended to include many other details of the visual system. Including ON- and OFF-center retinal cells, color processing, and spatio-temporal receptive fields are other possibilities which could be explored.

The demonstration of the very strong sensitivity to outliers of BCM and kurtosis, using the structure removal technique introduced in Chapter 4, makes a very strong claim about neural coding and the environment. Such rules are responding to a *very* small subset of the environment: the interesting parts of the environment are extremely rare. More work needs to be done to explore this property of the environment, and the learning rules, in order to understand what neurons are truly coding.

It has been an assumption of this work that any understanding of the origin of learning and memory in the visual system, should be general enough to be applied to other areas. This has been shown, at least partially, in several systems. Many of the experiments in LTP and LTD are done in hippocampus, and some are done in auditory cortex, where sounds are processed. More striking experiments have been performed which also lend themselves to the idea of fundamental processes in learning. In one such experiment, the outputs from the retina were rerouted to the auditory cortex, and the formation of *orientation selective* cells was observed (Sur et al., 1988). It is our belief that genetics uses a small set of tools, which are then molded by the environment in order to yield many of the properties we come to recognize in neural systems.

Though we have gained some understanding of learning and memory, we still have a long way to go to understand it fully. Many questions remain. How do different systems in the brain, which clearly interact strongly, actually communicate despite almost completely different input statistics? How do the

neurons code (and decode) the signals they receive? Can we understand such concepts as consciousness, creativity, or intuition, from the simple workings of individual neurons interacting? These questions and more are left for the future. While they slowly work out the details, we hope that people keep thinking of the big picture, and constantly examine the fundamental questions underlying this amazing organ we call the brain.

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