How asymmetries in the feedforward signals are exploited by target neurons to elaborate feature selectivity

Thesis Summary

Neurons in the primary visual cortex (V1) show sharp selectivity to stimulus features such as the orientation1, luminance increases and decreases2, colour3, spatial4 and temporal frequencies5. Broad biases for these stimuli are however already present sub-cortically and in some cases, as early as the retina6,7. For example, cortical inputs can arise from either the left or the right eye but cortical neurons themselves have a range of ocular dominances1 and selectivity for light increments or light decrements are established by the on and off bipolar cells in the retina but cortical neurons show varying range of selectivity to light increments and decrements8,9. In this thesis, we examine how visual neurons elaborate the feature selectivity established in the feedforward signal.

We studied feature selectivity in anaesthetized tree shrew and macaque visual neurons. Macaques are evolutionarily close to humans and their visual system has been studied extensively in an attempt to understand how we see. The tree shrew is a close ancestor of primates10. While in the macaques and cats, ocular dominance and stimulus polarity are organised in columns, in the tree shrews, these features are organised in layers11. However, neurons of similar orientation are still grouped in columns in the tree shrew supragranular layers12. Further, in the tree shrews, layer 4 neurons have similar receptive field properties as their LGN counterparts13,14 but layer 2/3 neurons show a similar degree of feature selectivity as reported in other species. As a result, there is a unique opportunity to explore the transformation that happens from LGN to layer 4 in cats (where most of the studies have been conducted) entirely within the cortex in the tree shrews. Hence, feature selectivity in the tree shrews were also studied.

We used optical imaging of intrinsic signals (OI) to image the response of cortical neurons to stimuli of different orientations (Chapter 3) to generate orientation maps. Different spatial filters were applied to separate the orientation responses of neuronal inputs and outputs. Single electrode recordings were used to map the topography of the imaged area. Single and multi-electrode recordings were also used to record the local field potentials (LFP) and multiunit activity of neurons.

We used single electrode recordings to record from the primary visual cortex (Chapter 4 and 6) and the superior colliculus (Chapter 5) of tree shrews to examine the relationship between orientation selectivity, spatial frequency tuning and linearity of spatial summation of neurons. Within the tree shrew, we also examined the transformation of orientation selectivity and spatial frequency tuning from layer 4 to layer 2/3, to identify the mechanism of orientation selectivity (Chapter 4).

## Chapter Outline

#### Chapter 1: Literature Review

The literature review is organised in three parts.

##### Visual Pathways

First the visual pathway from the retina through the LGN to V1 is described. The transformation of receptive field properties that occurs at each stage are also reviewed. An alternate pathway from the retina via the superior colliculus to the visual cortex is also described.

##### Mechanisms underlying feature selectivity

The mechanisms underlying the features studied in this thesis- orientation selectivity and spatial frequency tuning are critiqued. Specifically, the feedforward excitatory convergence model of Hubel and Wiesel (1962) proposed to explain orientation selectivity and alternate models of orientation selectivity are evaluated. The asymmetric LGN driven-recurrent model (ALD-RM; Vidysagar et al., 1996) is described.

##### Organisation of feature selectivity in the primary visual cortex

The organisation of feature selectivity in the primary visual cortex of the cats, macaques and tree shrews are described. Models through which the columnar organization of the cortex arise are also reviewed. A recent model that suggests that orientation selectivity arises from a limited number of broadly tuned channels is described.

#### Chapter 2: General Methods

In this chapter, the surgical and anaesthesia procedures, the stimuli used, stimulus presentation and data collection equipment and any data analysis that is commonly used in the chapters are described. A brief background on optical imaging of intrinsic signals (OI) is also presented.

#### Chapter 3: Radial Bias in the primary visual cortex of macaques

In this chapter, we examined the orientation biases of the geniculate inputs to the cortex. Optical imaging of intrinsic signals was used to record the orientation response of cortical neurons. The band-pass filtering commonly applied while analysing optical imaging data was not performed. We found that this unfiltered signal was tuned to only one orientation, namely the radial orientation. We then recorded from neurons using single electrodes and multi-electrode arrays and found that most of the LFP responses were tuned to the radial orientation whereas the multi-unit activity was tuned to a range of different orientations.

We suggest that the radial orientation represents the inputs to the cortex as a majority of the retinal neurons are tuned to the radial orientation and the unfiltered OI signal and the LFP tend to reflect the pre-synaptic activity rather than post-synaptic activity. Further, we suggest that the cortical neurons elaborate the full gamut of orientation selectivities observed in the cortex from a limited number of broadly tuned channels, with one of these channels tuned to the radial orientation.

#### Chapter 4: Mechanism of orientation selectivity in the tree shrew primary visual cortex

In this chapter, the transformation of receptive field properties from layer 4 to layer 2/3 was studied. We proposed that layer 2/3 neurons will generate both sharp orientation selectivity and band-pass spatial frequency tuning from the broadly tuned layer 4 neurons by providing orientation non-specific inhibition at lower spatial frequencies. We recorded the orientation and spatial frequency tuning responses from layer 2/3 and layer 4 of the tree shrew V1. We found that the layer 4 neurons showed broad orientation biases and low-pass spatial frequency tuning. Layer 2/3 neurons showed a bimodal distribution of orientation selectivity where some neurons showed sharp orientation selectivity while others showed broader orientation tuning. Overall, layer 2/3 neurons showed sharper orientation tuning than layer 4 neurons. A higher proportion of layer 2/3 neurons also showed band-pass spatial frequency tuning when compared to the layer 4 neurons. Further, we also showed that layer 4 and layer 2/3 neurons were tuned to the same orientation while neurons in layer 3c (sub-layer of layer 2/3 located just above layer 4) neurons were tuned to an orientation   60o away. Layer 4 neurons showed a greater degree of orientation selectivity at higher spatial frequencies. We hypothesised that the layer 2/3 neurons will fire best at the spatial frequency where the layer 4 neurons were sharply tuned to orientation but only found that this was true in 3 of the 18 neuron pairs. The possibility of layer 3c neurons providing cross-orientation inhibition to layer 2/3 neurons are further discussed.

#### Chapter 5: Receptive field properties of the tree shrew superior colliculus neurons

In this chapter, we examined the orientation and spatial frequency selectivity of neurons in the superficial layers of tree shrew superior colliculus (SC). We measured the orientation selectivity of the SC neurons using bars and gratings and the spatial frequency tuning of neurons in the shrew SC. We compared the results to those obtained from the tree shrew geniculo-striate system and hypothesised that if the neurons were similarly tuned to orientation and spatial frequency in both pathways, then it is likely that they inherited their properties from a common source, namely the retina. We found that a similar proporiton of SC and LGN neurons (Result published in Van Hooser et al., 2013) were biased for orientation and low-pass tuned to spatial frequency. As demonstrated in layer 4 (in chapter 4), the SC neurons were also more tuned for orientation at higher spatial frequencies. Our results indicate that orientation biases observed in the tree shrew LGN and layer 4 are likely to have originated from the same source.

#### Chapter 6: Is the tree shrew primary visual cortex a linear filter?

In this chapter, we recorded the spatial frequency tuning responses from V1 simple cells in the shrew and evaluated if they function as linear filters. It has been controversial whether cortical simple cells function as edge detectors or as fourier analysers when processing visual information. Studies have shown that simple cells in cats and macaques analyse the visual scene in both the space and spatial frequency domains. Here we examined if the shrew V1 neurons functioned as linear filters or as edge detectors and found that simple cells in the tree shrews were far better Fourier analysers than their counterparts in the macaque and cat cortex.

#### Chapter 7: General Discussion

The results obtained from the previous chapters are discussed in the context of generation of feature selectivity as well as the organisation of feature selectivity in the primary visual cortex. A comparison of the visual systems of the cats, macaques and tree shrews is also undertaken.