Literature Review/ Background:

Plan:

Part 1: The Visual Pathway

1. Retino-geniculate-striate cortex.
2. Alternative pathways
3. Cross Species comparison.

Part 2: Receptive field properties

1. Orientation selectivity
2. Spatial Frequency Tuning
3. Relationship between orientation selectivity and Spatial Frequency Tuning
4. Linearity of Spatial Summation
   1. Tolhurst and Dean, 1990: Sometimes, simple cells show essential non-linearities- push-pull model of receptive field organisation- cat striate cortex.  
      -Look up Tanaka 1983- that receptive .  
      Suggest that simple cells can only show modulated response at low spatial frequencies at high contrasts. This is not true. Linear simple cells show a modulated response at all spatial frequencies. But complex cells actually fit in with this description.  
      Push-pull model: Simple cell sub-regions receive both excitatory and inhibitory inputs that allow some simple cells to act linearly while others don’t.
   2. Shapley et al., 1981: In macaques: show that there are X and Y cell parallel pathways. X cells are found in the magno and parvo cellular layers but Y cells are only found in magno layers. Magno layers are related to contrast processing while parvo cells are concerned with wavelength detection: likely the macaque RGCs confer their properties onto the LGN neurons.
   3. DeMonasterio 1978: Macaque Retinal Ganglion Cells: X and Y cells. X cells: tended to have longer conduction latencies, less transient responses to small stimuli and more central retinal distribution than Y cells. X/Y divide indicates the degree of linear spatial summation of cone inputs.
   4. Tanaka 1983: questions: hierarchical model? Do simple cells and complex cells receive linear vs non-linear inputs? Do simple cells receive single or double row projections?  
      Geniculo-striate cross correlation method. Didn’t find any complex cells in layer 4?
5. Cross-Species Comparison

**Mechanisms of Orientation Selectiviy**

**The tree shrew primary visual cortex**

Part two of this thesis focuses on the primary visual cortex (V1) of the tree shrews. While extensive studies have been conducted in the cat and macaque primary visual cortices, relatively few have been conducted in the tree shrew visual system. Here the evidence presented in the earlier studies are summarised.

**Laminar Organisation**

V1 of tree shrews has a similar laminar organisation to its macaque and cat counterparts as outlined in the schematic below (Figure 1). For our purposes, inputs from the LGN terminate in Layers 4a, 4b and 3c/3b (References). The projections from layer 4 to layer 2/3 are further organised with the outer edges of Layer 4 projecting to layer 3c, the middle areas of layers 4a and 4b projecting to layer 3b and the inner areas of layers 4a and 4b, close to the binocular region projecting to the more dorsal regions of layer 3 and layer 2.

Other anatomical studies suggest that Horizontal projections in layer IIIc, and layers 2 and 3 a and b.

Inputs to layer four vary in their origins and physiological properties. are segregated into on, off and W cell inputs respectively. Majority of the inputs to the striate cortex in the tree shrews are from X-like cells, which show a sustained response to stimulus and show linear summation over their receptive field areas. Most of the neurons in Layer 4a and 4b receive inputs from the contralateral eye and with the central area containing binocular cells.

Orientation selectivity of the neurons.

Originally all layers had a proportion of orientation selective neurons (Humphrey and Norton, 1980 a). See figure 2.

While this figure shows that when using a bar, most neurons are indeed tuned to orientation, there are a large proportion of unoriented neurons in layers 3 and 4. But using bars, orientation tuning is sharper as bar contains higher spatial frequency components. Later studies using gratings showed that majority of the neurons in the tree shrew Layer 4 were not tuned to orientation and resembled their LGN counterparts in orientation selectivity. See Figure 3. While we will see in chapters 2 and 3 that the spatial frequency tuning and stimulus used is important for characterising orientation selectivity, these studies were important establishing that the orientation selectivity of layer 4 neurons were similar to that of LGN neurons. This means that orientation tuning in the tree shrew V1 is similar to that seen in macaque parvocellular system. While in the magnocellular system, Layer 4Ca neurons are sharply tuned to orientations, in parvocellular system, 4Cb neurons are untuned to orientations at lower spatial frequencies and sharp orientation tuning only arises in layers 2/3 of the cortex. In line with this, there have also been reports of on and off subpathways in the parvocellular system.

**Columnar organisation of orientiaton selectivity**

Autoradiographic and ephys studies showed that there were columns of orientation organised in strips perpendicular to the V1/V2 border in tree shrews. But later optical imaging studies showed that this organisation was seen in the borders of the primary visual cortex not in the centres. In the middle the organisation was similar to that observed in the primary visual cortex of cats and macaques, with similarly oriented neurons grouped in columns and converging in pinwheel centres.

**Mechanisms of Orientation Selectivity**

Early studies conducted in the tree shrew primary visual cortex indicated that orientation tuning in the V1 of tree shrews may be generated from excitatory convergence of unoriented, layer 4 neurons onto layer 2/3 neurons. However, the authors acknowledged that while this excitatory convergence is capable of providing orientation biases, the extensive horizontal connections present in the superficial layers of the tree shrew play an important role in sharpening these orientation biases (Chisum et al., 2003; Mooser et al., 2004). Later however, it was shown that layer 4 neurons did not have circular receptive fields as was originally thought but had broad orientation biases (Van Hooser et al., 2013). A separate study by Veit et al (2014) also argued that horizontal connections in tree shrews are important as just the orientation tuning of inputs seemed insufficient to predict the degree of orientation selectivity of the layer 2/3 cells.

Huang et al (2014) when they tried to test how the horizontal connections worked, didn’t really find what they had hoped. Found that horizontal connections contributed linearly to cell responses regardless of the orientations of where the horizontal connection terminated. They also did not find any axial effects as has been predicted in the past. Issues- they could just be stimulating within 500 microns, where horizontal connections are not specific? Recurrent excitation? Also they could selectively activate only excitatory neurons using their viral vectors which could leave and inhibitory modulatory circuits out.

Recently, using two photon calcium imaging, Lee et al, 2016, suggested that off inputs to the cortex are established by on inputs organising themselves around off inputs which establish topography. However, there are a few caveats to this model. Muly and Fitzpatrick (1992) showed that on and off inputs to layer 2/3 cells have significant overlap. Further, Veit et al (2014) showed that only 7% of all cells in the shrew V1 had segregated receptive field sub-divisions, lacking the basic RF structure for the majority of the cells to develop orientation selectivity using this method.