Radial Bias Literature Review

Vidyasagar and Eysel 2015

Even for orientation selectivity-

* Excitatory Convergence
* Intracortical Cross Orientation Inhibition
* Intracortical iso-orientation facilitation.
* Mild orientation selectivity already present in the retinal inputs.

**Follow up on these**

Orientation selectivity of synaptic input to neurons in mouse and cat primary visual cortex. Tan et al., 2011; J. Neuroscience.

Retinal specification of cortical orientation selectivity.

Cruz-Martin, A. et al. (2014) A dedicated circuit linking direction selective retinal ganglion cells to primary visual cortex. Nature 507, 358–361

Stone, J. (1978) The number and distribution of ganglion cells in the cat’s retina. J. Comp. Neurol. 180, 753–772

Anderson, P.A. et al. (1988) The overall pattern of ocular dominance bands in cat visual cortex. J. Neurosci. 8, 2183–2200

Follow up:Sharma et al 2001

Show that when the visual inputs are routed to the auditory cortex, the auditory cortex develops orientation tuning and columns.

Katz, L. C. & Shatz, C. J. Synaptic activity and the construction of cortical circuits. Science 274, 1133±

1138 (1996).

Yuste, R. & Sur, M. Development and plasticity of the cerebral cortex: from molecules to maps. J.

Neurobiol. 41, 1±6 (1999).

Kim, D.-S. & Bonhoeffer, T. Reverse occlusion leads to a precise restoration of orientation preference

maps in visual cortex. Nature 370, 370±372 (1994).

9. Godecke, I. & Bonhoeffer, T. Development of identical orientation maps for two eyes without

common visual experience. Nature 379, 251±254 (1996).

10. Ruthazer, E. & Stryker,M. P. The role of activity in development of long range horizontal connections

in area 17 of the ferret. J. Neurosci. 16, 7253±7269 (1996).

Leventhal 1983

Cats, Primary Visual Cortex,

Found that +15 degs- neurons tuned to radial orientation

Found that 4-15 degs- less radial orientation bias

Less than 4 degrees- not so much

* More cells for the horizontal meridian and vertical meridian.
* These cells will be tuned to the horizontal and vertical meridians if they had radial bias
* This could account for the over-representation of the horizontal and vertical orientations as well- oblique effect
* Recent fMRI studies have demonstrated the radial bias in the visual cortex. Studies by Sasaki et al, etc have shown that when shown obliquely oriented stimulus, the activity in the BOLD response is higher than that observed for the horizontal and vertical stimuli. These studies show the radial bias on a larger and cruder spatial scale. Here, the radial bias in the cortex has been demonstrated at a smaller scale and a higher resolution, relating optimum orientations to receptive field locations rather than whole hemispheres. Sasaki et al. (2006) also demonstrate that the radial bias exists at higher visual areas. Our own results suggest that the inputs to the extrastriate areas from V1 will be tuned to the radial and the orthogonal orientations. These results along with our results indicate that the radial bias plays an important role in establishing cortical architecture.
* If they are inputs, this is what it means for orientation selectivity.
* Other optical imaging studies that have examined orientation biases have demonstrated the oblique effect; that is an underrepresentation of the oblique orientations in the primary visual cortex. These studies examined biases by grouping pixels based on their responses to different orientation but did not examine their relationship with their receptive field locations. Where the relationship between the receptive field location and the orientation of the neurons was, a radial bias was reported every time and at every stage of the visual system. In some cases, a horizontal bias has been reported due to the presence of the horizontal streak in the retina but even in these animals, as one goes further away from the horizontal streak and the fovea, a strong radial bias is observed.
* The radial bias might be an inevitable effect in the visual system. The prevalence of the radial bias has been higher in the peripheral visual system. Psychophysical studies have shown that the oblique effect is a very strong effect. The neurophysiological correlates of these oblique effects have been unclear but the radial bias in the periphery seems to be a result of the way in which the eye grows, automatically elongating the ganglion cell dendritic fields which influence their responses to oriented stimuli. The oblique effect in perception and the radial bias on the neural level may be unrelated phenomena.
* A new theory (Vidyasagar and Eysel, 2015) suggested that both the orientation tuning of cortical neurons and cortical architecture can be established by sharpening biases that originate earlier in the visual system.
* Let us examine the way the visual system processes colour data. Colour is encoded in the retina by cones with broad sensitivities that act in an opponent manner to each other. So, there is the red/ green opponent system and blue/ yellow opponent system encoded by the L, M and S cones. These cones are activated by a light over a large range of wavelengths. Neurons in the primary visual cortex (V1) that are tuned to colour however, show a sharp selectivity to colour (REFERENCE). This tuning in the primary visual cortex arises from a sharpening of the broader bias established in the retina. A similar mechanism has been reported for other features that have been observed in the V1. Neuronal properties such as ocular dominance and phase selectivity (on/off) can all be explained by biases established by biases observed in the retina. A similar mechanism may be proposed for orientation selectivity.
* The case of orientation selectivity is more complex than ocular dominance or phase selectivity. The nature of ocular dominancy and phase selectivity is such that the seed for their tuning in the retina is quite intuitive and commonly accepted. Inputs may either be from the right eye or the left eye. They may arise from a ganglion cell that receives inputs from an on or off bipolar cells. These biases are well characterised in the literature. In the case of orientation selectivity however, the sub-cortical biases are not so obvious. While many studies have shown that sub-cortical neurons are indeed biased for orientation (eg: see Levick and Thibos, 1980; Vidyasagar and Urbas, 1982) it is still not widely accepted. Several studies continue to argue that orientation selectivity is first generated in the primary visual cortex through some variant of the excitatory convergence model. Further, the exact nature of the bias is still questioned. Some studies suggest that there is radial orientation bias in the retina. Some others suggest that there is a preponderance of the horizontal and vertical orientation biases (the oblique effect). Rovamo et al (1978) showed an eccentricity dependence of perceptual bias with the central vision showing oblique effect and peripheral vision showing the radial bias. One study in the cat area 17 showed that first order neurons in layer 4 of the cortex were tuned to cardinal orientations. Cardinal orientations were defined as vertical, horizontal or radial. It could be that the retinal neurons are tuned for one of these cardinal orientations which are reflected in the first order neurons in the cat visual cortex.
* If the range of orientation selectivity seen in the primary visual cortex originates from biases observed in the subcortical areas, we predicted that the inputs to the cortex may be broadly tuned to a small number of
* While several theories have been posited for both these properties of the primary visual cortical neurons separately, few explain both properties simultaneously. Recent theory proposes that both the cortical architecture and the properties of individual neurons can arise from limited number of broadly tuned thalamic inputs. In this chapter, we aimed to test this theory using optical imaging of intrinsic signals (OI). We examined the orientation selectivity of the neurons and proposed that the broad range of orientation selectivities seen in the primary visual cortex arise from inputs that are broadly tuned to a small number of orientations.
* fMRI and electrophys studies show Radial angle
* What is shown in the results: radial angle on a large spatial.
* LFPs tuned to the radial angle
* What does the LFP mean?
* Probably- both are synaptic and presynaptic activity
* Which= inputs?
* A significant feature of the primary visual cortex is that neurons are sharply tuned to orientation and similarly tuned neurons are organised in cortical columns. Since it’s report by Hubel and Wiesel (1962; 1968) the mechanism underlying orientation selectivity of cortical neurons has been widely debated. Hubel and Wiesel (1962) postulated a theory of excitatory convergence where unoriented geniculate inputs arranged in a row lead to sharp orientation selectivity. Several studies have since shown that this model does not explain all the properties of cortical neurons such as contrast invariance of orientation tuning and the role of inhibition through horizontal connections in the cortex (References). This model also disregards orientation biases that have been reported in the sub-cortical areas (References). No theory unifying
* Against this backdrop,
* and Wiesel suggested their excitatory convergence model for orientation tuning. This model suggests that orientation tuning in the primary visual cortex is established by the feedforward convergence of inputs from neurons arranged in a row in the lateral geniculate nucleus (LGN). Now, the orientation selectivity and the columnar architecture is a widely accepted characteristic of the primary visual cortex of most species (see mouse work for an alternative scheme, (Reference)). However, the question remains as to whether both these properties arise from the same mechanism.
* A study by Sur et al. (2001) showed that simple feedforward mechanisms were not effective in establishing the columnar architecture observed in the primary visual cortex. Where they routed signals from the V1 to the auditory cortex, they found that orientation tuning was sharpened (although not enough) by the feedforward mechanism but the cortical architecture of V1 was not reflected in the auditory cortex, implying that intracortical intervention was necessary for establishing cortical architecture as we know it.
* Radial bias has been demonstrated in the retina, LGN and V1 of cats, macaques and humans using electrophysiological, anatomical and imaging studies. Levick and Thibos showed that neurons in the cat retina had elongated dendritic fields that were arranges a spokes of a wheel with the area centralis being the axis. This elongation could be caused by the growth of the eye outward.
* The oblique effect has been reported in human psychophysics and extracellular electrophysiology. Appelle (1972) indicated that behavioural studies in all animals, from humans to octopuses, showed a bias for the horizontal and vertical orientations. Electrophysiological studies have also demonstrated the prevalence of the oblique effect in the cat LGN (Vidyasagar and Urbas, 1982) and striate cortex (Orban and Kennedy, 1981; Payne and Berman, 1983; Pettigrew et al., 1968; Vidyasagar and Henry, 1990; Li et al., 2003); the macaque V1 (Kennedy et al., 1985; Mansfield, 1974; Mansfield and Ronner, 1978) and the ferrets (Chapman et al., 1998; Coppola et al., 1998; Grabska-Barwinska et a., 2009). Both behavioural and electrophysiological studies that reported the oblique effect show that the effect is strongest in central vision with the peripheral vision showing a weaker oblique effect (Mansfield, 1974) or a strong radial bias (Rovamo et al., 1980).
* Studies that reported the oblique effect did not carefully find the relationship of the receptive field location to the visual field locus. Where this has been done, the radial bias has been reported on every occasion (REFERENCES). However, this does not indicate that the existence of the oblique effect contradicts the radial bias. In cats and humans, there are reports of a horizontal streak, a zone of high retinal ganglion cell density that runs along the horizontal meridian representation in the retina. This could translate to a large number of neurons in the LGN and the striate cortex being tuned to horizontal orientation at least. This is reflected in electrophysiological studies that show that the bias for horizontal orientations is stronger than the bias for the vertical orientations (Reference).
* inputs to the primary visual cortex and found that inputs to the primary visual cortex were strongly biased for the radial orientation. This fits in with the hypothesis that the orientation bias observed in the inputs were derived from biases observed in the retina rather than being generated by excitatory convergence of unoriented LGN inputs arranged in a row. However, we predicted that we would observe a bias for more than one of the cardinal orientations. This was not evident in the veridical signal. The filtered signal however, showed a bias to the radial orientation and the orientation orthogonal to the radial orientation. Not sure what this is about.