

0.1 Notes

Most geniculate neurons are excited by neurons of the same type- mixes only with respect to sustained/transient type (Cleland et al., 1971)

Visual pathway of sustained/ transient remains separate from retina all the way to the cortex (Cleland et al., 1971).

(Malach, Amir, Harel, & Grinvald, 1993) Macaques Optical Imaging and biocytin injections- Found connections between same eye neurons. Binocular neurons projected to binocular neurons. Orientation not as fidel. Less projections to orthogonal orientations.

(Maldonado, Godecke, Gray, & Bonhoeffer, 1997) Cats Cells in pinwheel centres have a similar degree of orientation selectivity as the neurons in isoorientation domains. Pinwheels are where all the different orientation domains converge.

(Hubel & Wiesel, 1969) macaques Electrode penetrations- orientation and ocular dominance columns (Bartfeld & Grinvald, 1992) Macaques Pinwheels at the border between ocular dominance columns. CO blobs also on the border between OD columns but did not co-incide with the pinwheels. Cortical hypercolumn consisting of two OD columns and two pinwheel centres.

They also showed that the cortical RF structure is not elongated when using spots of light but rather circular. The bar responses using bars is actually elongated because the bar might activate some of the inhibitory regions. Does not say inhibition is cross orientation- rather that inhibition comes from the same orientation.

Intracellular inhibition tuned to the same orientation as the neurons orientation (Anderson, Carandini, & Ferster, 2000).

Does not really explain orientation selectivity- could at best sharpen orientation selectivity.

(Priebe & Ferster, 2006) Cats, Threshold can explain the effects of cross-orientation suppression. Don't really explain the effects of Eysel et al.

(Kisvárdy, Tóth, Rausch, & Eysel, 1997) Cats, Traced the horizontal connections- majority of excitatory and inhibitory connections to iso-orientation domains (40%). More in support of an overall non-specific inhibition from pooled responses.

(Morrone, Burr, & Maffei, 1982):Cats, Used Noise of optimal orientation and stimuli of orthogonal orientation- Found cross orientation inhibition- better for simple cells than complex cells. Inhibition in most orientations, facilitation in the same orientation- inhibition pooled from many cortical neurons? Spatial frequency also pooled across many different SFs.

(Wörgötter & Eysel, 1988; Eysel, Crook, & Machemer, 1990) Cats Area 17: Recorded from a neuron while suppressing activity in neurons located 500 microns away from the recorded neuron- found that orientation tuning broadened in the recorded neuron. Evidence for inhibition from neurons of other orientations due to the periodicity of cortical orientation tuning. Broadening of orientation selectivity due to an increase in firing rate at the orthogonal orientation.

(Crook & Eysel, 1992): As above but in Area 18. More inhibition from neurons that are tuned 45 degrees apart than less than 22.5 degrees apart. When iso-orientation inhibition- causes increase in firing rate more than anything else.

(Sharon & Grinvald, 2002): With Grinvald- showed that orientation of the neurons are potentially inherited from the feedforward signal but the amplification involves both intracortical excitation and inhibition in cats, VSDs.

(Somers, Nelson, & Sur, 1995) Computational modelling- neuron received weakly tuned thalamic signal, strong iso-orientation inhibition, weak cross orientation inhibition and no shunting inhibition. Found that neurons were sharply

tuned to orientation. Suggest that inhibition occurs in an orientation non-specific manner. Orientation tuning is an emergent property of the cortex.

Another explanation

1) Orientation selectivity is sharply tuned to orientation - Pei et al., 1994? Showed that input was broadly tuned to orientation. Cortical cooling experiments- not cool cortex enough? Kara et al, vs. Viswanathan et al. 2) LGN inputs to different simple cells- read the original papers. 3) Layer wise organisation of simple and complex cells- not really- first order complex cells. 4) disinhibition.

Issues of the excitatory convergence model and key opponents.

Adjusted excitatory convergence model Priebe and Ferster- feedforward + non-linearities.

Recurrent models

(Somers et al., 1995; Douglas, Koch, Mahowald, Martin, & Suarez, 1995). Further, it was suggested that instead of just subtractive inhibition, if shunting inhibition was employed, the network was more stable (Heeger 1992, 1993, Carandini & Heeger 1994, Chance & Abbott 2000).

(Adorján, Levitt, Lund, & Obermayer, 1999) No need for biases in the feedforward inputs- can be generated completely from intracortical mechanisms.

(Carandini & Ringach, 1997) Modelled Somers and Douglas and found that with recurrent excitation alone, the model was really bad at distinguishing between orientations. Requires sharply tuned inhibition. Non-specific inhibition doesn't really work. This is opposite of what what has been reported.

1) anatomy: neurons receive mostly intracortical, excitatory connections. 2) Dynamics: Dynamics of orientation selectivity show that neurons get more and more tuned to orientation as time progresses- Pei et al., 1994; Ringach 2002. 3) Intracortical inhibition- inhibition tuned to the same orientation as the excitation.

(Nelson & Turrigiano, 1998) Galaretta and Hestrin show that prolonged firing causes a much bigger depression at excitatory synapse rather than at inhibitory synapses.

Early evidence for the recurrent excitation model comes from (Shu, Hasenstaub, & McCormick, 2003): Invitro slices- showed that excitation and inhibition were balanced.

(Monier, Chavane, Baudot, Graham, & Frégnac, 2003): Most excitatory and inhibitory connections are tuned to the same orientation as the recorded neuron.

(Li, Ibrahim, Liu, Zhang, & Tao, 2013): Intracortical excitatory circuits linearly amplify the thalamocortical information and may influence the size of the receptive field by recruiting additional inputs

(Sato, Haider, Häusser, & Carandini, 2016) Neural networks give shunting inhibition by moderating the level of excitation than by increasing inhibition.

(Tan, Brown, Scholl, Mohanty, & Priebe, 2011) mouse and cats- inhibition is the same orientation as excitation. Sharpening of orientation selectivity by changes in input conductances.

(Shapley, Hawken, & Xing, 2007) INtracortical inhibition is important for orientations selectivity.

0.2 Orientation Selectivity

(De Valois, William Yund, & Hepler, 1982): Macaques neurons in V1 are tuned to orientation and direction. Different degrees of orientation selectivity within simple/complex cells. Within foveal neurons, vertical and horizontal orientations are better represented. Most inhibition at orientations adjacent to the orthogonal orientation rather than at the orthogonal orientation- models.

(Frégnac & Imbert, 1978) kittens- sharp orientation selectivity from 12 days already but ocular dominance takes some time. Also binocular inputs required

to generate the full range of orientations preferences in kittens. kittens under 3 weeks of age a higher proportion of binocular neurons. Horizontal and vertical biases in early stages of development.

(Sherk & Stryker, 1976) Also kittens- sutured eyes= recorded at 22-23 days- already tuned to orientation.

(Cynader, Berman, & Hein, 1975) Cats reared in a room with unidirectionally moving stimuli- direction selectivity- direction of the moving grating (leftward). Most units were oriented vertically. No such effect in the SC.

0.3 Spatial Frequency Tuning

(Skottun, Bradley, Sclar, Ohzawa, & Freeman, 1987) Contrast invariant spatial frequency tuning.

(R. L. DeValois, Albright, & Thorell, 1982) Described the old modulation ratio. Striate cells have quite narrow band pass spatial frequency bandwidths, at a given retinal eccentricity, the distribution of peak frequency covers a wide range of frequencies. Foveal samples extend into higher spatial frequencies as do complex cells- this last bit doesn't make sense as generally complex cells are bigger and so have lower spatial frequencies.

(Vidyasagar & Mueller, 1994) Showed that neurons in the primary visual cortex started responding at lower spatial frequencies when Bicuculline was applied. orientation non-specific inhibition to neurons.

(Meese & Hess, 2004) Cross orientation inhibition is more visible at lower spatial frequencies.

(Bredfeldt & Ringach, 2002) Suppression at lower spatial frequencies. Temporally delayed. Talks about the two component model?

(Bauman & Bonds, 1991) Orientation non-specific, spatial frequency specific inhibition. Inhibition from a pool of simple cells with spatially incoherent

receptive fields as inhibition doesn't have a temporal component. Temporal component of inhibition?

Temporal frequency 3Hz.

Sharply tuned inhibition to evoke tuned inhibition? problem in causality- but as in ALD-RM, atleast the low spatial frequency inhibition is already tuned.

Inhibition is cross channel?

(Morrone et al., 1982) Inhibition is broadly tuned for spatial frequency.

(DeAngelis, Robson, Ohzawa, & Freeman, 1992) Suppression is broadly tuned for spatial frequency.

(David, 2004) When using natural images, the spatial frequency tuning of the inhibition undergoes complex changes.

(K. K. DeValois & Tootell, 1983) Used gratings of peak spatial frequency and other spatial frequency masks. Inhibition is spatial frequency specific and at higher and lower spatial frequencies. Probably serves a different function than/ in addition to sharpen spatial frequency tuning.

(Field & Tolhurst, 1986) Simple cell receptive fields could be modelled by Gabor functions that had 3 free parameters- Envelope width, carrier width and carrier frequency.

(R. L. DeValois et al., 1982) Described the old modulation ratio. Striate cells have quite narrow band pass spatial frequency bandwidths, at a given retinal eccentricity, the distribution of peak frequency covers a wide range of frequencies. Foveal samples extend into higher spatial frequencies as do complex cell- this last bit doesn't make sense as generally complex cells are bigger and so have lower spatial frequencies (Fig6). Receptive field size of complex cells only have a very small relationship with the peak spatial frequency- not a direct X/Y relationship. In simple cells the relationship is more obvious.

(Silverman, Gross, De Valois, & Elfar, 1989) Found a continuum of spatial

frequencies rather than two distinct groups- high spatial and low spatial frequencies. Lower spatial frequency neurons were found in cytochrome oxidase blobs.

(Born & Tootell, 1991) Peak spatial frequencies split into two groups, low and high sf, blob and interblob areas. Low pass in blob areas and high pass in interblob areas.

(Webster & De Valois, 1985) Receptive field models, like those proposed by Hubel and Wiesel do not explain the relative independence of spatial frequency and orientation tuning. More likely the receptive fields can be modelled using a two dimensional Gabor model or a gaussian derivative.

Spatial frequency and receptive fields and simple and complex cells.

(Xing, Ringach, Shapley, & Hawken, 2004) Global spatial frequency tuning variables. Correlated better with global orientation selectivity variables- suggesting that they are more correlated than non-global variables- global= looks at the whole curve. Local= look at the tuning around the peak. Suggest that the strong correlation is due to similar intracortical mechanisms underlying both the measurements. (Parker & Hawken, 1988)- High spatial frequency cut-off-size of the smallest subunit

(Sirovich & Uglesich, 2004) No obvious spatial frequency columns- each location was a combination of low and high spatial frequency stimuli.

(Malone, Kumar, & Ringach, 2007) Width and spatial period of receptive fields decrease by 15%. This narrowing could explain the low spatial frequency attenuation observed.

Evidence for a H&W like convergence.

(Frazor, Albrecht, Geisler, & Crane, 2008) Dynamics of spatial frequency tuning: Results due to latency effects. Latency is positively correlated with spatial frequency that means at higher spatial frequencies, the latencies were

higher.-

H&W like excitatory convergence could explain these results.

(Allen & Freeman, 2006) Suggest that the spatio-temporal dynamics observed in the LGN could explain the dynamics observed in the cortex- especially, if there is centre-surround delay in LGN neurons and convergent inputs from multiple cells with different receptive field sizes and response latencies.

These results maynot necessarily be contradictory to the results of the ringach studies. other studies show that a basic selectivity is established in the LGN and the cortex sharpens this. 2) the ALD-RM model suggests that multiple neurons do converge on to the same neuron- just with overlapping receptive fields.

(Purushothaman, Chen, Yampolsky, & Casagrande, 2014) Looked at the dynamics of spatial frequency tuning. Two groups of neurons: Group 1- optimum sf increases monotonically. Group 2- Optimum sf changed non-monotonically- first increased then decreased. Group 1: Monotonic shift occurred even without the presence of low spatial frequency suppression. Non-monotonic shift - high spatial frequency suppression is always present. Neural mechanism could be cortical or sub-cortical in nature?

(Nirouy, 2014) Modelled development of spatial frequency selectivity. Verify results of (Allen & Freeman, 2006) suggesting that the higher center-surround delays result in stronger cortical shifts. spatial component such as center and surround size and relative surround strength play a strong role in cortical spatial frequency tuning. Alitto and Usrey 2003, Briggs and Usrey 2008, Andolina et al., 2012- cortical feedback has been shown to strengthen the LGN center-surround relationship.

Cortico-thalamic feedback loop- functions to modulate surround strength- which in turn skews the spatial frequency tuning to higher spatial frequencies.

(Cudeiro & Sillito, 1996) cortico-geniculate feedback enhanced the surround

antagonism on centre response in the geniculate. X cells, surround suppression more tuned to lower spatial frequencies. - feedback at these spatial frequencies? feedback of the cortical level analysis refines the transfer of the visual input at geniculate level in a stimulus-context-dependent fashion.

References

- Adorján, P., Levitt, J. B., Lund, J. S., & Obermayer, K. (1999). A model for the intracortical origin of orientation preference and tuning in macaque striate cortex. *Visual Neuroscience*, *16*(2), 303–318. doi: 10.1017/S0952523899162114
- Allen, E. A., & Freeman, R. D. (2006). Dynamic Spatial Processing Originates in Early Visual Pathways. *Journal of Neuroscience*, *26*(45), 11763–11774. doi: 10.1523/JNEUROSCI.3297-06.2006
- Anderson, J. S., Carandini, M., & Ferster, D. (2000). Orientation Tuning of Input Conductance , Excitation , and Inhibition in Cat Primary Visual Cortex. *Journal of neurophysiology*, *84*, 909–926.
- Bartfeld, E., & Grinvald, A. (1992). Relationships between orientation-preference pinwheels, cytochrome oxidase blobs, and ocular-dominance columns in primate striate cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *89*(24), 11905–9.
- Bauman, L. A., & Bonds, A. B. (1991). Inhibitory refinement of spatial frequency selectivity in single cells of the cat striate cortex. *Vision Research*, *31*(6), 933–944. doi: 10.1016/0042-6989(91)90201-F
- Born, R. T., & Tootell, R. B. H. (1991). Spatial frequency tuning and surrounding inhibition of single cells in macaque supragranular striate cortex.

- Proceedings of the National Academy of Sciences*, 88, 7066–7070.
- Bredfeldt, C. E., & Ringach, D. L. (2002). Dynamics of Spatial Frequency Tuning in Macaque V1. , 22(5), 1976–1984.
- Carandini, M., & Ringach, D. L. (1997). Predictions of a recurrent model of orientation selectivity. *Vision Research*, 37(21), 3061–3071. doi: 10.1016/S0042-6989(97)00100-4
- Crook, J. M., & Eysel, U. T. (1992). GABA-induced inactivation of functionally characterized sites in cat visual cortex (area 18): Effects on orientation tuning. *The Journal of Neuroscience*, 12(5), 1625–1816.
- Cudeiro, J., & Sillito, A. M. (1996). Spatial frequency tuning of orientation-discontinuity-sensitive corticofugal feedback to the cat lateral geniculate nucleus. *J Physiol (Lond)*, 490 (Pt 2, 481–492.
- Cynader, M., Berman, N., & Hein, A. (1975). Cats raised in a one-directional world: Effects on receptive fields in visual cortex and superior colliculus. *Experimental Brain Research*, 22(3), 267–280. doi: 10.1007/BF00234769
- David, S. V. (2004). Natural Stimulus Statistics Alter the Receptive Field Structure of V1 Neurons. *Journal of Neuroscience*, 24(31), 6991–7006. doi: 10.1523/JNEUROSCI.1422-04.2004
- De Valois, R. L., William Yund, E., & Hepler, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research*, 22(5), 531–544. doi: 10.1016/0042-6989(82)90112-2
- DeAngelis, G. C., Robson, J. G., Ohzawa, I., & Freeman, R. D. (1992). Organization of suppression in receptive fields of neurons in cat visual cortex. *J Neurophysiol*, 68(1), 144–163. doi: 1517820
- DeValois, K. K., & Tootell, R. B. H. (1983). Spatial frequency inhibition in cat striate cortex. *Journal of Physiology*, 336, 359–378.
- DeValois, R. L., Albright, D. G., & Thorell, L. G. (1982). Spatial Frequency

- Selectivity of Cells in Macaque Visual Cortex. *Vision research*, 22, 545–559.
- Douglas, R., Koch, C., Mahowald, M., Martin, K. A., & Suarez, H. H. (1995). Recurrent excitation in neocortical circuits. *Science*, 269(5226), 981–985. doi: 10.1126/science.7638624
- Eysel, U., Crook, J., & Machemer, H. (1990). GABA-induced remote inactivation reveals cross-orientation inhibition in the cat striate cortex. *Experimental Brain Research*, 80, 626–630.
- Field, D., & Tolhurst, D. (1986). The structure and symmetry of simple-cell receptive-field profiles in the cat’s visual cortex. *Proceedings of the Royal Society of London*, 228, 379–400.
- Frazor, R. A., Albrecht, D. G., Geisler, W. S., & Crane, A. M. (2008). Visual Cortex Neurons of Monkeys and Cats : Temporal Dynamics of the Spatial Frequency Response Function. *Journal of Neurophysiology*, 91(6), 2607–2627. doi: 10.1152/jn.00858.2003
- Frégnac, Y., & Imbert, M. (1978). Early development of visual cortical cells in normal and dark-reared kittens: relationship between orientation selectivity and ocular dominance. *Journal of Physiology*, 278, 27–44.
- Hubel, D. H., & Wiesel, T. N. (1969). Anatomical demonstration of columns in the monkey striate cortex. *Nature*, 221(5182), 747–750. doi: 10.1038/221747a0
- Kisvárdy, Z. F., Tóth, É., Rausch, M., & Eysel, U. T. (1997). Orientation-specific relationship between populations of excitatory and inhibitory lateral connections in the visual cortex of the cat. *Cerebral Cortex*, 7(7), 605–618. doi: 10.1093/cercor/7.7.605
- Li, Y. T., Ibrahim, L. A., Liu, B. H., Zhang, L. I., & Tao, H. W. (2013). Linear transformation of thalamocortical input by intracortical excitation. *Nature*

Neuroscience, 16(9), 1324–1330. doi: 10.1038/nn.3494

- Malach, R., Amir, Y., Harel, M., & Grinvald, A. (1993). Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. *Proceedings of the National Academy of Sciences*, 90(22), 10469–10473. doi: 10.1073/pnas.90.22.10469
- Maldonado, P. E., Godecke, I., Gray, C. M., & Bonhoeffer, T. (1997). Orientation selectivity in pinwheel centers in cat striate cortex. *Science*, 276(June), 1551–1555.
- Malone, B. J., Kumar, V. R., & Ringach, D. L. (2007). Dynamics of Receptive Field Size in Primary Visual Cortex. , 1563, 407–414. doi: 10.1152/jn.00830.2006.
- Meese, T. S., & Hess, R. F. (2004). Low spatial frequencies are suppressively masked across spatial scale, orientation, field position, and eye of origin. *Journal of vision*, 4(10), 843–859. doi: 10.1167/4.10.2
- Monier, C., Chavane, F., Baudot, P., Graham, L. J., & Frégnac, Y. (2003). Orientation and direction selectivity of synaptic inputs in visual cortical neurons: A diversity of combinations produces spike tuning. *Neuron*, 37(4), 663–680. doi: 10.1016/S0896-6273(03)00064-3
- Morrone, M., Burr, D., & Maffei, L. (1982). Functional Implications of Cross-Orientation Inhibition of Cortical Visual Cells. I. Neurophysiological Evidence. *Proceedings of the Royal Society B: Biological Sciences*, 216(1204), 335–354. doi: 10.1098/rspb.1982.0078
- Nelson, S. B., & Turrigiano, G. G. (1998). Synaptic depression: a key player in the cortical balancing act. *Nature Neuroscience*, 1(7), 539–541.
- Nirody, J. A. (2014). Development of spatial coarse-to-fine processing in the visual pathway. *Journal of Computational Neuroscience*, 36(3), 401–414.

doi: 10.1007/s10827-013-0480-6

- Parker, A. J., & Hawken, M. J. (1988). *Two-dimensional spatial structure of receptive fields in monkey striate cortex*. (Vol. 5) (No. 4). doi: 10.1364/JOSAA.5.000598
- Priebe, N. J., & Ferster, D. (2006). Mechanisms underlying cross-orientation suppression in cat visual cortex. *Nature Neuroscience*, 9(4), 552–561. doi: 10.1038/nn1660
- Purushothaman, G., Chen, X., Yampolsky, D., & Casagrande, V. A. (2014). Neural mechanisms of coarse-to-fine discrimination in the visual cortex. *Journal of Neurophysiology*, 112(11), 2822–2833. doi: 10.1152/jn.00612.2013
- Sato, T. K., Haider, B., Häusser, M., & Carandini, M. (2016). An excitatory basis for divisive normalization in visual cortex. *Nature Neuroscience*, 19(4), 568–570. doi: 10.1038/nn.4249
- Shapley, R., Hawken, M., & Xing, D. (2007). The dynamics of visual responses in the primary visual cortex. *Progress in Brain Research*, 165, 21–32. doi: 10.1016/S0079-6123(06)65003-6
- Sharon, D., & Grinvald, A. (2002). Dynamics and Constancy in Cortical Spatiotemporal Patterns of Orientation Processing. *Science*, 295, 512–515.
- Sherk, H., & Stryker, M. P. (1976). Quantitative Study of Cortical Orientation Selectivity in Visually Inexperienced Kitten. *Journal of neurophysiology*, 39(1), 63–70.
- Shu, Y., Hasenstaub, A., & McCormick, D. A. (2003). Turning on and off recurrent balanced cortical activity. *Nature*, 393, 288–293. doi: 10.1038/nature01614.1.
- Silverman, M. S., Grosof, D. H., De Valois, R. L., & Elfar, S. D. (1989). Spatial-frequency organization in primate striate cortex. *Proceedings of the Na-*

- tional Academy of Sciences of the United States of America*, 86(January), 711–715. doi: 10.1073/pnas.86.2.711
- Sirovich, L., & Uglesich, R. (2004). The organization of orientation and spatial frequency in primary visual cortex. *Proceedings of the National Academy of Sciences*, 101(48), 16941–16946. doi: 10.1073/pnas.0407450101
- Skottun, B. C., Bradley, A., Sclar, G., Ohzawa, I., & Freeman, R. D. (1987). The effects of contrast on visual orientation and spatial frequency discrimination: a comparison of single cells and behavior. *J Neurophysiol*, 57(3), 773–786.
- Somers, D. C., Nelson, S. B., & Sur, M. (1995). An emergent model of orientation selectivity in cat visual cortical simple cells. *The Journal of neuroscience*, 15(8), 5448–65.
- Tan, A. Y. Y., Brown, B. D., Scholl, B., Mohanty, D., & Priebe, N. J. (2011). Orientation Selectivity of Synaptic Input to Neurons in Mouse and Cat Primary Visual Cortex. *The Journal of Neuroscience*, 31(34), 12339–12350. doi: 10.1523/JNEUROSCI.2039-11.2011
- Vidyasagar, T. R., & Mueller, a. (1994, jan). Function of GABAA inhibition in specifying spatial frequency and orientation selectivities in cat striate cortex. *Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale*, 98(1), 31–8. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/8013589>
- Webster, M. A., & De Valois, R. L. (1985). Relationship between spatial-frequency and orientation tuning of striate-cortex cells. *Journal of the Optical Society of America A*, 2(7), 1124–1132. doi: 10.1364/JOSAA.2.001124
- Wörgötter, F., & Eysel, U. T. (1988). Inhibitory and excitatory contributions of orientation tuning in the cat’s striate cortex. *Society of Neuroscience*

Abstract, 326(8).

Xing, D., Ringach, D. L., Shapley, R., & Hawken, M. J. (2004). Correlation of local and global orientation and spatial frequency tuning in macaque V1. *Journal of Physiology*, 557(3), 923–933. doi: 10.1113/jphysiol.2004.062026