Surround modulation by long-range lateral connections in an orientation map model of primary visual cortex development and function

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1. Introduction

Neuronal response properties are often smoothly topographically organised across the cortical surface. The prototypical example is the map of orientation preference in primary visual cortex (V1). Many models of orientation map development have been very successful in reproducing the features of biological maps. The majority of these models are based on a principle of short-range excitatory and long-range inhibitory connections between neurons, e.g. von der Malsburg, 1973, Swindale, 1992, Obermayer et al., 1990 and the LISSOM model, Sirosh and Miikkulainen, 1997.
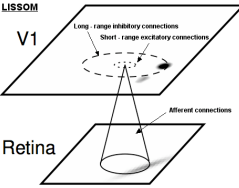
However, biological data suggests that long-range connections between V1 neurons arise primarily from putatively excitatory pyramidal cells (Gilbert & Wiesel,1989, Hirsch & Gilbert, 1991, Weliky et al.,1995, Angelucci et al.,2002). Furthermore, simple models with long-range excitation and short-range inhibition have shown how a biologically realistic circuitry can reproduce features of adult V1 function such as extra-classical receptive field phenomena (Schwabe et al., 2006).

These models of adult function suggest that long-range excitatory connections are facilitatory when input is at low contrast, yet stronger activation of local inhibitory neurons at high contrast will cause these connections to act suppressively. Previous developmental map models with long-range inhibitory connections are therefore unable to account for aspects of surround modulation. However, it is not yet clear how such circuits can arise, which parts of the system are plastic, or in general how to reconcile these findings with otherwise successful developmental models such as LISSOM.

We present the first model which is consistent with this realistic connectivity, yet also reproduces the features of successful developmental models of topographic map formation. Future work will address how this connectivity can lead to surround modulation both in adult V1 and throughout development.

2. Model Architecture

- Based on the reduced LISSOM model (Miikkulainen et al. 2005).
- Neurons are modeled as firing rate-based point neuron units.
- Initial afferent receptive field weights are random and lateral weights have an isotropic Gaussian distribution.
- Final organisation is achieved after 20,000 input presentations (randomly oriented and positioned Gaussian patterns).
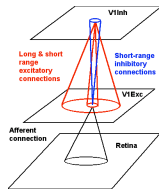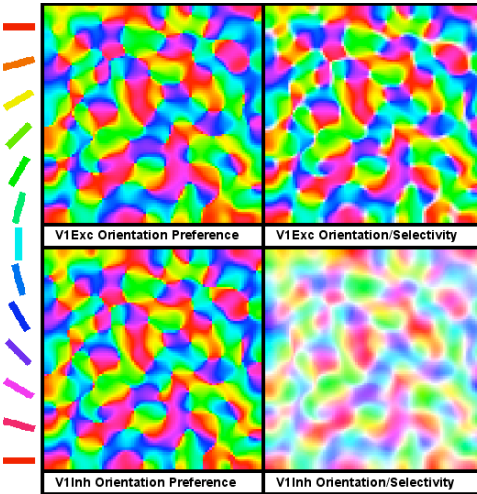
3. Activation and Learning

- Neurons combine activation from each projection using the following activation equation:

$$\eta_{ij}(t) = \sigma\left(\sum_p \gamma_p \sum_{kl \in RF_p} X_{kl}(t-1)\omega_{kl,ij}\right)$$

- The sigmoidal output function(σ) for each excitatory neuron is adapted by a homeostatic plasticity mechanism (Treisch, 2005) which brings its firing rate distribution into an approximately exponential regime (Joint work with Veldri Kurniawan).

- Afferent and long range projection weights are adjusted by unsupervised Hebbian learning with divisive normalisation :

$$\omega_{kl,ij}(t+1) = \frac{\omega_{kl,ij}(t) + \alpha\eta_{ij}X_{kl}}{\sum(\omega_{kl,ij}(t) + \alpha\eta_{ij}X_{kl})}$$

4. Results
Orientation Maps

V1Exc Orientation Preference | V1Exc Orientation/Selectivity
V1Inh Orientation Preference | V1Inh Orientation/Selectivity

- Realistic (and similar) orientation maps in both V1Exc (colour indicates orientation preference) and V1Inh. Pinwheel centres, saddle points, fractures, and linear zones are all observed.
- Orientation selectivity of inhibitory neurons (strength of colour indicates selectivity) is much lower overall than excitatory neurons.

Receptive fields & Lateral Connections

Afferent
V1Exc Lateral Excitatory
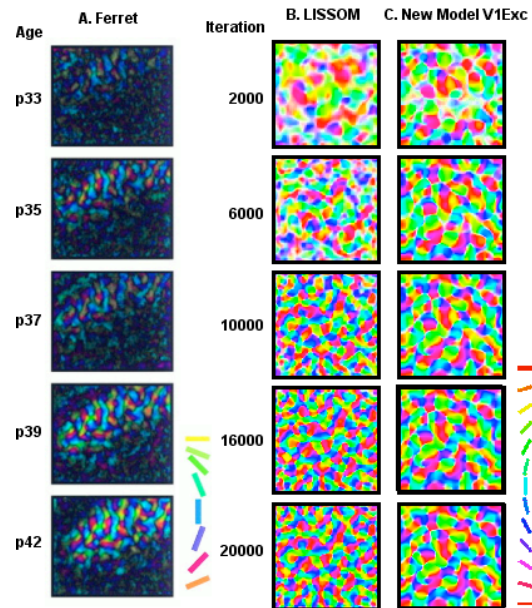V1Inh Lateral Excitatory

Retina
V1Exc | V1Inh
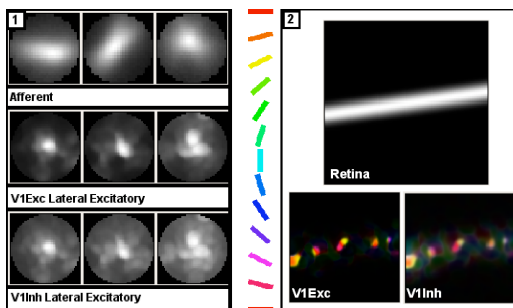
- Nearly all self organised afferent receptive fields are elongated and orientation selective. Lateral connections in V1Exc are dense around the neuron and patchy at longer distances. In V1Inh these connections are more diffuse overall. (Figure 1)
- The response to an oriented line on the retina (Figure 2) is patchy and selective for this orientation. In V1Inh activity patterns are similar but have a broader "halo" of activation.

Development

- Experimentally observed orientation maps appear to arise as a stable structure that is maintained throughout development (A - from Chapman et al., 1996).
- During development in LISSOM and other self-organising models, the orientation map structure changes dramatically over time (B).
- The new model (C) makes several changes to LISSOM which make development more stable over time. Output function threshold changes in LISSOM are replaced by homeostatic plasticity and short-range connections no longer shrink during the learning process.

Orientation preference & selectivity

Age	A. Ferret	Iteration	B. LISSOM	C. New Model V1Exc
p33		2000		
p35		6000		
p37		10000		
p39		16000		
p42		20000		

5. Discussion

Parameters in the model have been chosen such that presentation of input patterns results in activity patterns in V1Exc and V1Inh which are similar yet broader overall in V1Inh. During Hebbian learning, similar activity patterns will lead to the development of similar lateral connections and therefore smooth self-organisation and map formation. The broader overall activity in V1Inh also leads to a lower overall orientation selectivity in inhibitory neurons.

We believe that this broader inhibition acts at high-contrast as an effective "Mexican-hat", equivalent to the long range inhibition in previous models (such as LISSOM). However, such models are be unable to account for low-contrast inputs, where the dynamics of inhibition will be different.

Contributions

1. This model is the first developmental model of orientation map formation with connectivity compatible with experimental results.
2. This is the first model with stable development of an orientation map over time.
3. This model will facilitate investigation of surround modulation in neurons that each have a specific, dynamic connectivity embedded in a realistic map structure.
4. The realistic connectivity in this new model now allows parameters to be tied to specific experimental results in particular species.

Future Work

- Lateral excitatory connections depend on map structure, for example, connections between similar orientation preference domains in Tree Shrew V1 is shown in figures A&B (Bosking et al. 1997). Using this new model, which can reproduce both the facilitatory and supressive properties of long-range excitatory connections, it is now possible to investigate surround modulation in neurons with unique connectivity embedded within a map, both in adult and developing V1.
- Species differences in orientation map structure and their possible effects on functions such as surround modulation can be investigated.
- Other future work includes adding feedback connections from higher visual areas and using natural image input patterns.
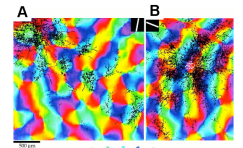
Conclusions

- This model shows for the first time that it is possible to develop realistic maps in a way that is compatible with biologically realistic connectivity.
- This model is a good platform for the understanding of surround modulation and its dependence on lateral interactions in both the adult and developing visual cortex.

6. Acknowledgements

References

von der Malsburg, C. (1973). Self-organization of orientation-sensitive cells in the striate cortex. Kybernetik, 15:85–100.
Swindale, N. V. (1992). A model for the coordinated development of columnar systems in primate striate cortex. Biological Cybernetics, 66:217–230
Obermayer, K., Ritter, H., and Schulten, K. (1990d). A principle for the formation of the spatial structure of cortical feature maps. Proceedings of the National Academy of Sciences, USA, 87:8345–8349.
Sirosh, J., and Miikkulainen, R. (1997). Topographic receptive fields and patterned lateral interaction in a self-organizing model of the primary visual cortex. Neural Computation, 9:577–594
Gilbert, C. D., and Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. The Journal of Neuroscience, 9:2432– 2442.
Hirsch, J. A., and Gilbert, C. D. (1991). Synaptic physiology of horizontal connections in the cat's visual cortex. The Journal of Neuroscience, 11:1800–1809.
Weliky, M., Kandler, K., Fitzpatrick, D., and Katz, L. C. (1995). Patterns of excitation and inhibition evoked by horizontal connections in visual cortex share a common relationship to orientation columns. Neuron, 15:541–552.
Angelucci, A., Levitt, J. B., and Lund, J. S. (2002a). Anatomical origins of the classical receptive field and modulatory surround field of single neurons in macaque visual cortical area V1. Progress in Brain Research, 136:373–388.
Schwabe, L., Obermayer, K., Angelucci, A. and Bressloff P. C. (2006). The role of feedback in shaping the extra-classical receptive field of cortical neurons: a recurrent network model. The Journal of Neuroscience, 26(36):9117-29.
Miikkulainen, R., Bednar, J., Choe, Y., and Sirosh, J. (2005). Computational maps in the visual cortex. Springer, Berlin.
Treisch, J., (2005) A Gradient Rule for the Plasticity of a Neuron's Intrinsic Excitability. ICANN 2005, Lecture Notes in Computer Science 3696:65–70.