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, Welsby 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 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 surrounding 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:

  \[ a_i = \sum_j w_{ij} v_j + \text{bias}_i \]

- The sigmoidal output function \( \gamma \) for each excitatory neuron is adapted by a homeostatic plasticity mechanism (Trisch, 2005) which brings its firing rate distribution into an approximately exponential distribution.

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

  \[ w_{ij}(t+1) = w_{ij}(t) + \eta \frac{u_i(t) u_j(t)}{\text{Bias}_i (t) + \sum_k u_k(t)} \]

- Near 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 V1h activity patterns are similar but have a broader “halo” of activation.

4. Results Orientation Maps

- Realistic (and similar) orientation maps in both V1Exc (colour indicates orientation preference) and V1Inh (Pinehede 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. (Figure 3)

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.

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This work has been carried out using the new Topographica simulator available freely from www.topographica.org

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.

Contributions

1. This model is the first developmental model of orientation map formation with connectivity compatible with experimental results.
2. This model provides a better 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 cortical setting.
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 (Boxing et al. 1997). Using this new model, which can reproduce both the facilitatory and suppressive 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.

References