Exploring the Functional Significance of Dendritic Inhibition In Cortical Pyramidal Cells

M. W. Spratling and M. H. Johnson
Centre for Brain and Cognitive Development, Birkbeck College, London. UK.

Abstract

Inhibitory synapses contacting the soma and axon initial segment are commonly presumed to participate in shaping the response properties of cortical pyramidal cells. Such an inhibitory mechanism has been explored in a large and influential class of computational model. However, the majority of inhibitory synapses target the dendrites of pyramidal cells, and recent physiological data suggests that this dendritic inhibition affects tuning properties. We describe a model that can be used to investigate the role of dendritic inhibition in the competition between neurons. This model has demonstrated that dendritic inhibition significantly enhances the computational and representational properties of neural networks.

Keywords: Dendrites, inhibition, competition, receptive fields, tuning.

1 Introduction

Lateral inhibition between cortical cells is known to play an important role in determining the receptive field properties of those cells [4, 11]. Such lateral inhibition provides a mechanism through which neurons compete to respond to the current pattern of stimulation. It is generally assumed that lateral inhibition targets the soma or axon initial segment and virtually all neural network models make use of this kind of competitive inhibitory mechanism [6, 7, 8, 14, 15, 20, 22, 25, 29, 31, 32]. While inhibitory synapses do contact the soma and axon initial segment [19, 26], the vast majority (93%) of inhibitory synapses targeting neocortical pyramidal cells terminate on the dendrites [3, 5].

Somatic inhibition can be equally effective at suppressing responses to excitatory inputs stimulating any part of the dendritic tree [28]. In contrast, dendritic inhibition is likely to have strong effects only on more distal inputs along the same dendritic branch [1, 12, 13, 21, 23, 28], and will thus selectively inhibit specific groups of excitatory inputs. Hence, while somatic inhibition non-selectively inhibits responses to all stimuli, dendritic inhibition selectively inhibits specific patterns of excitatory inputs. Recent physiological data suggests that the latter mechanism is important in determining the tuning properties of cortical pyramidal cells [33]. It has been shown that the blockade of GABAergic synapses in monkey inferotemporal cortex (area TE) results in specific disinhibition of responses to particular stimulus features rather than removal of non-specific inhibition [33]. Hence, this data suggests that dendritic inhibition plays a role in determining the response properties of pyramidal cells. We thus introduce a neural network which can explore the role of dendritic inhibition as a mechanism of competition between pyramidal cells.

2 Method

Figure 1(a) illustrates the architecture used by conventional models of lateral inhibition. In some implementations competition is achieved (as shown) by using explicit lateral connections between the nodes of the network [6, 7, 15, 25, 29, 31], while in others competition is implemented implicitly through a selection process which chooses the 'winning' node(s) [8, 14, 22, 32]. In all of these algorithms nodes attempt to 'block' other nodes from generating a response to the current stimulus. A node's success in this competition is dependent on the total strength of the stimulation it receives and nodes which compete unsuccessfully have their output activity suppressed. This architecture can thus be seen to model the effects of lateral inhibition targeting the soma or axon initial segment.

Figure 1(b) shows the architecture of our model of dendritic inhibition. As with the conventional models we simplify reality by assuming that the role of inhibitory interneurons can be approximated

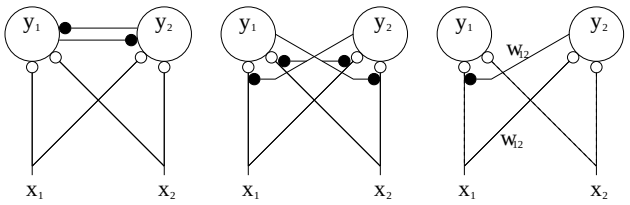

Figure 1: Models of lateral inhibition. Simple, two-node, networks are presented to illustrate models using different mechanisms of lateral inhibition. Nodes are shown as large circles, excitatory synapses as small open circles and inhibitory synapses as small filled circles. (a) The standard model of lateral inhibition provides competition between outputs. (b) The model of dendritic inhibition provides competition for inputs. (c) The model of dendritic inhibition with only one lateral weight shown. This lateral weight is given the same value (w_{12}) as the afferent weight shown as a solid line.

by direct inhibitory connections between excitatory neurons. Furthermore, we group together all the synapses contributing to a dendritic compartment to form a single input to the node. Dendritic inhibition is then modeled as (linear) inhibition of this input. This mechanism thus enables nodes to selectively inhibit other nodes from responding to particular input features.

3 Results

By making the lateral weights equal in strength to the corresponding afferent weights (as shown in figure 1(c)) each node can 'block' its preferred inputs from activating other nodes. With this arrangement of weights, if a node is strongly activated by the overall stimulus and it has a strong synaptic weight to a certain feature of that stimulus, then it will inhibit other nodes from responding to that feature. On the other hand, if an active node receives only weak weights from a feature then it will only weakly inhibit other nodes from responding to that specific feature. Hence, if individual nodes have learnt weights that are selective to certain stimuli then when multiple stimuli are simultaneously

presented to the network each of the nodes representing one of these stimuli can be simultaneously active. Unlike networks using the conventional mechanism of lateral inhibition there are no restrictions on the number of active nodes that can be simultaneously active, and hence a network using dendritic inhibition can respond appropriately to any combination of input patterns.

A network in which nodes compete using dendritic inhibition also deals naturally with stimuli which share sub-features in common (*i.e.*, patterns which overlap in the input space). This is important since in many situations distinct sensory events will share many features in common. If such situations are to be distinguished then it is necessary for different sets of neurons to respond despite this overlap in input features. Both these properties are illustrated in figure 2. In this example six nodes each represent one of six patterns defined across six input features (labelled 'a' to 'f'). Each node responds exclusively to its preferred input pattern despite the strong overlap between stimuli and multiple nodes responds when multiple stimuli are presented.

Competition not only makes responses more selective (in the short-term), but since learning is activity-dependent it also makes the receptive fields of individual nodes more distinct (in the long-term). Improved response properties result in more correct learning episodes [15], and hence, the advantageous coding properties that arise from using dendritic inhibition can result in efficient, unsupervised, learning [27]. For example, to learn the weights shown in figure 2 required, on average, 55 training cycles (equivalent to approximately 9 presentations of each of the six patterns). This compares favourably to a network using the conventional method of lateral inhibition which requires 3000 pattern presentations to find such a solution [15] .

Discussion

A network of neurons competing through dendritic lateral inhibition is capable of generating correct representations based on the 'knowledge' stored in the synaptic weights of the neural network.

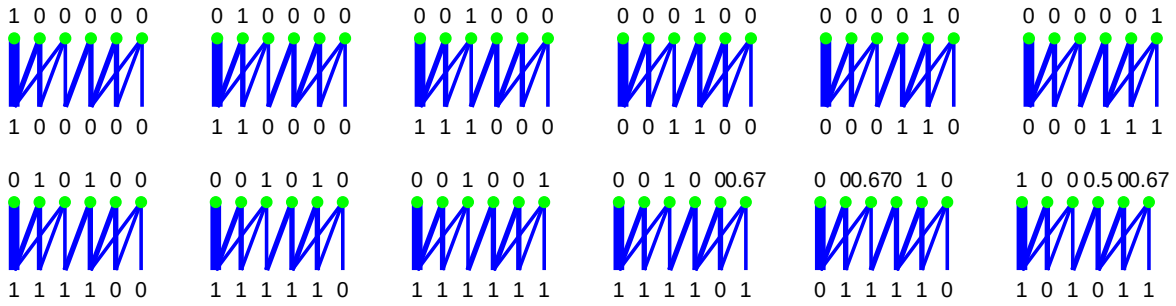

Figure 2: Representing multiple, overlapping, input patterns. A network consisting of six nodes receiving six inputs (‘a’, ‘b’, ‘c’, ‘d’, ‘e’, and ‘f’) is wired up so that nodes are selective to the patterns ‘a’, ‘ab’, ‘abc’, ‘cd’, ‘de’, and ‘def’. The response of the network to each of these input patterns is shown on the top row. Dendritic inhibition (lateral weights have been omitted from the figures) enables each node to respond exclusively to its preferred pattern. In addition, the response to multiple and partial patterns is shown on the bottom row. Pattern ‘abcd’ causes the nodes representing ‘ab’ and ‘cd’ to be active simultaneously, despite the fact that this pattern overlaps strongly with pattern ‘abc’. Input ‘abcde’ is parsed as ‘abc’ together with ‘de’, and input ‘abcdef’ is parsed as ‘abc’ + ‘def’. Input ‘abcdf’ is parsed as ‘abc’ + two-thirds of ‘def’, hence the addition of ‘f’ to the pattern ‘abcd’ radically changes the representation that is generated. Input ‘bcde’ is parsed as two-thirds of ‘abc’ plus pattern ‘de’. Input ‘acef’ is parsed as ‘a’ + one half of ‘cd’ + two-thirds of pattern ‘def’.

Specifically, it is capable of generating a local encoding of individual input patterns as well as responding simultaneously to multiple patterns, when they are present, in order to generate a factorial or distributed encoding. It can produce an appropriate representation even when patterns overlap and respond to partial patterns such that the response is proportional to how well that input matches the stored pattern. Not only can dendritic inhibition provide appropriate coding properties it can be used to efficiently learn such representations.

Our architecture assumes that all afferent synapses, carrying information about a feature of the

input space, can be modelled as a single input to a node. This can be justified since it is presumed that related synapses cluster together within dendritic trees so that local operations are performed by multiple, functionally distinct, dendritic subunits before integration at the soma [9, 10, 13, 17, 18, 23, 24]. Dendritic inhibition could thus act to 'block' the output from individual functional compartments. It has long been recognized that a dendrite composed of multiple subunits would provide a significant enhancement to the computational powers of an individual neuron [16, 17, 18] and that dendritic inhibition could contribute to this enhancement [12, 13, 24]. However, the role of dendritic inhibition in competition between cells and its subsequent effect on neural coding and receptive field properties has not previously been investigated.

The idea embodied in our model is that pyramidal cells inhibit the activity of dendritic compartments in other pyramidal cells within the same cortical area. It has been shown that cortical pyramidal cells innervate inhibitory cell types which in turn form synapses on the dendrites of pyramidal cells [2, 30]. Our model predicts that it should be possible to find pairs of pyramidal cells for which action potentials generated by one cell induce inhibitory post-synaptic potentials within the dendrites of the other. More complex models, which include a separate inhibitory cell population, and which use multi-compartmental models of dendritic processes could relate our proposal more directly with physiology. We hope that our demonstration of the computational and representational advantages that could arise from dendritic inhibition will serve to stimulate such more detailed studies.

Acknowledgements

This work was funded by MRC Research Fellowship number G81/512.

References

[1] L. T. Borg-Graham, C. Monier, and Y. Fregnac. Visual input evokes transient and strong shunting inhibition in visual cortical neurons. *Nature*, 393(6683):369–73, 1998.

[2] E. H. Buhl, G. Tamas, T. Szilagyi, C. Stricker, O. Paulsen, and P. Somogyi. Effect, number and location of synapses made by single pyramidal cells onto aspiny interneurones of cat visual cortex. *The Journal of Physiology,*, 500(3):689–713, 1997.

[3] J. DeFelipe and I. Fariñas. The pyramidal neuron of the cerebral cortex: morphological and chemical characteristics of the synaptic inputs. *Progress in Neurobiology*, 39(6):563–607, 1992.

[4] U. T. Eysel, I. A. Shevelev, N. A. Lazareva, and G. A. Sharev. Orientation tuning and receptive field structure in cat striate neurons during local blockade of intrcortical inhibition. *Neuroscience*, 84(1):25–36, 1998.

[5] J. Fiala and K. Harris. Dendritic structure and spines. In G. Stuart, N. Spruston, and M. Häusser, editors, *Dendrites*, chapter 1, pages 1–34. Oxford University Press, Oxford, 1999.

[6] P. Földiák. Adaptive network for optimal linear feature extraction. In *Proceedings of the IEEE/INNS International Joint Conference on Neural Networks*, volume 1, pages 401–5, New York, 1989. IEEE Press.

[7] P. Földiák. Forming sparse representations by local anti-hebbian learning. *Biological Cybernetics*, 64:165–70, 1990.

[8] S. Grossberg. Competitive learning: from interactive activation to adaptive resonance. *Cognitive Science*, 11:23–63, 1987.

[9] M. Häusser. Synaptic function: dendritic democracy. *Current Biology*, 11:R10–2, 2001.

[10] M. Häusser, N. Spruston, and G. J. Stuart. Diversity and dynamics of dendritic signalling. *Science*, 290(5492):739–44, 2000.

[11] B. Jagadeesh. Inhibition in inferotemporal cortex: generating selectivity for object features.

Nature Neuroscience, 3(8):749–50, 2000.

[12] C. Koch, T. Poggio, and V. Torre. Nonlinear interactions in a dendritic tree: localization, timing, and role in information processing. *Proceedings of the National Academy of Science USA*, 80 (9):2799–802, 1983.

[13] C. Koch and I. Segev. The role of single neurons in information processing. *Nature Neuroscience*, 3(supplement):1171–7, 2000.

[14] T. Kohonen. *Self-Organizing Maps*. Springer, Berlin; London, 1997.

[15] J. A. Marshall. Adaptive perceptual pattern recognition by self-organizing neural networks: context, uncertainty, multiplicity, and scale. *Neural Networks*, 8(3):335–62, 1995.

[16] B. W. Mel. Synaptic integration in an excitable dendritic tree. *Journal of Neurophysiology*, 70 (3):1086–101, 1993.

[17] B. W. Mel. Information processing in dendritic trees. *Neural Computation*, 6:1031–85, 1994.

[18] B. W. Mel. Why have dendrites? A computational perspective. In G. Stuart, N. Spruston, and M. Häusser, editors, *Dendrites*, chapter 11, pages 271–89. Oxford University Press, Oxford, 1999.

[19] V. B. Mountcastle. *Perceptual Neuroscience: The Cerebral Cortex*. Harvard University Press, Cambridge, Massachusetts; London, 1998.

[20] R. C. O'Reilly. Six principles for biologically based computational models of cortical cognition. *Trends in Cognitive Sciences*, 2(11):455–62, 1998.

[21] W. Rall. Theoretical significance of dendritic trees for neuronal input-output relations. In R. F. Reiss, editor, *Neural Theory and Modeling*, pages 73–97. Stanford University Press, Stanford, California, 1964.

[22] D. E. Rumelhart and D. Zipser. Feature discovery by competitive learning. *Cognitive Science*, 9:75–112, 1985.

[23] I. Segev. Dendritic processing. In M. A. Arbib, editor, *The Handbook of Brain Theory and*

Neural Networks, pages 282–9. MIT Press, Cambridge, Massachusetts; London, 1995.

[24] I. Segev and W. Rall. Excitable dendrites and spines: earlier theoretical insights elucidate recent direct observations. *Trends in Neurosciences*, 21(11):453–60, 1998.

[25] J. Sirosh and R. Miikkulainen. Cooperative self-organization of afferent and lateral connections in cortical maps. *Biological Cybernetics*, 71:66–78, 1994.

[26] P. Somogyi and K. A. C. Martin. Cortical circuitry underlying inhibitory processes in cat area 17. In D. Rose and V. G. Dobson, editors, *Models of the Visual Cortex*, chapter 54. Wiley, Chichester, 1985.

[27] M. W. Spratling and M. H. Johnson. Pre-integration lateral inhibition enhances unsupervised learning. submitted.

[28] N. Spruston, G. Stuart, and M. Häusser. Dendritic integration. In G. Stuart, N. Spruston, and M. Häusser, editors, *Dendrites*, chapter 10, pages 231–271. Oxford University Press, Oxford, 1999.

[29] N. V. Swindale. The development of topography in the visual cortex: a review of models. *Network: Computation in Neural Systems*, 7(2):161–247, 1996.

[30] G. Tamas, E. H. Buhl, and P. Somogyi. Fast IPSPs elicited via multiple synaptic release sites by different types of GABAergic neurone in the cat visual cortex. *The Journal of Physiology,*, 500 (3):715–38, 1997.

[31] C. von der Malsburg. Self-organisation of orientation sensitive cells in the striate cortex. *Kybernetik*, 14:85–100, 1973.

[32] G. Wallis. Using spatio-temporal correlations to learn invariant object recognition. *Neural Networks*, 9(9):1513–9, 1996.

[33] Y. Wang, I. Fujita, and Y. Murayama. Neuronal mechanisms of selectivity for object features revealed by blocking inhibition in inferotemporal cortex. *Nature Neuroscience*, 3(8):807–13, 2000.