

Cortical region interactions and the functional role of apical dendrites

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Abstract

The basal and distal apical dendrites of pyramidal cells occupy distinct cortical layers and are targeted by axons originating in different cortical regions. Hence, apical and basal dendrites receive information from distinct sources. Physiological evidence suggests that this anatomically observed segregation of input sources may have functional significance. This possibility has been explored in various connectionist models that employ neurons with functionally distinct apical and basal compartments. A neuron in which separate sets of inputs can be integrated independently has the potential to operate in a variety of ways which are not possible for the conventional model of a neuron in which all inputs are treated equally. This article thus considers how functionally distinct apical and basal dendrites can contribute to the information processing capacities of single neurons and, in particular, how information from different cortical regions could have disparate affects on neural activity and learning.

Keywords: Cerebral cortex, Pyramidal cells, Dendrites, Neural Networks, Attention, Learning, Memory, Perception.

1 Introduction

The cerebral neocortex has a laminar structure which is conventionally classified into six layers. Distinct areas or regions of the cortical sheet can also be identified on the basis of anatomical and functional differences. Pyramidal cell bodies are found in all regions and in layers II, III, V, and VI. This class of neuron has a distinctive morphology, as illustrated in Figure 1, that is characterized by two separate dendritic arbors: the basal dendrites which occupy the same layer as the cell body, and the apical dendrites which ascend into more superficial layers. For pyramidal cells in layer VI the apical dendrite extends to layer IV (Miller, 1996), for pyramidal cells in all other layers the apical dendrite extends to layer I (Figure 2). The pyramidal cell is the most abundant type of cortical neuron (Mountcastle, 1998). In addition, it is the only class of neuron to project outside the cortex (Crick and Asanuma, 1986) and is the primary source of connections between different cortical areas (Braitenberg, 1978). This class of cell is thus likely to have a major role in cortical information processing.

The axons of pyramidal cells can form long-range projections to other cortical regions (and to sub-cortical structures) (Crick and Asanuma, 1986; Ebdon, 1996; Mountcastle, 1998). In general, cortical regions are reciprocally connected (Crick and Asanuma, 1986; Felleman and Van Essen, 1991; Kastner and Ungerleider, 2000; Lamme et al., 1998; Mountcastle, 1998). The layer of origin and of termination of these associative connections allows them to be classified as ascending (feedforward) or descending (feedback), as shown in Figure 2 (Barbas and Rempel-Clower, 1997; Budd, 1998; Crick and Koch, 1998; Ebdon, 1996; Felleman and Van Essen, 1991; Johnson and Burkhalter, 1997; Lamme et al., 1998; Mountcastle, 1998; Mumford, 1992). The feedforward connections are provided by axon projections from pyramidal cells in layers II and III. These projections terminate predominantly in layer IV of the higher region (as do inputs from the thalamus). The main target for feedforward projections are spiny-stellate cells which, in turn, target the basal dendrites of pyramidal cells in layers II and III. Feedback connections are provided by the axon projections from pyramidal cells in layers V and VI and terminate mainly in layers I and VI of the lower region (or are sent to sub-cortical structures). The main targets of feedback projections terminating in layer I are the apical dendrites of pyramidal cells with somata in layers II, III and V (Budd, 1998; Cauller, 1995; Rockland, 1998; Rolls and Treves, 1998).

It is thus the case that the apical and basal dendrites of pyramidal cells are targeted by axons originating in different cortical areas. Hence, the apical and basal dendrites receive information from different sources.

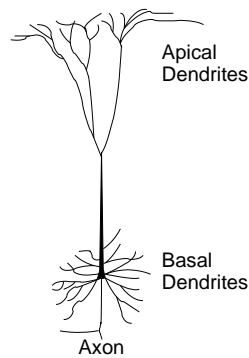


Figure 1: A pyramidal cell. Pyramidal cells are the predominant class of excitatory neuron in the cerebral cortex. The detailed dendritic morphology of pyramidal cells is highly variable, however, one relatively consistent feature is the segregation into two distinct dendritic projections: the apical dendrite which extends towards more superficial cortical layers, and the basal dendrites which extend laterally within the same layer as the cell body. Adapted from (Paré et al., 1998).

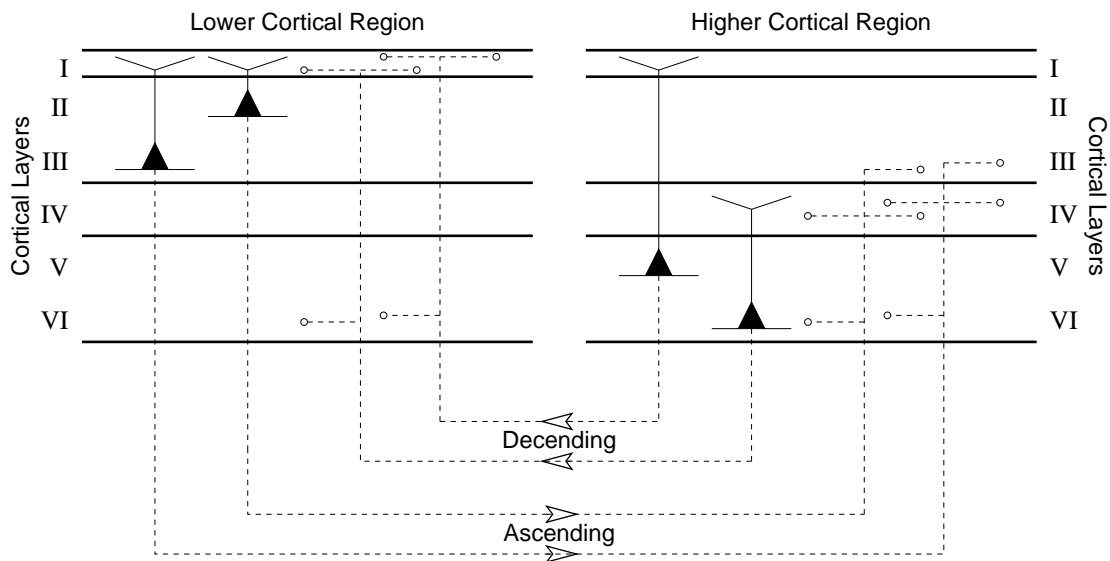


Figure 2: Cortical layers and regions. A schematic showing pyramidal cells within the six layers of the cortical sheet. Pyramidal cell bodies are shown as filled triangles, dendrites as solid lines and axons as dashed lines. All other cell types have been omitted, as has the intra-regional connectivity. The cortical sheet is shown divided into two regions at different levels in an information processing hierarchy. Axon projections connecting these two regions are illustrated.

For example, the pyramidal cells in layers II and III receive feedforward information at the basal dendrites and feedback information at the apical dendrites. This article attempts to explore why the cortical anatomy is arranged in this way. It reviews both theoretical and experimental data which, taken together, suggest that the segregation of input sources targeting apical and basal dendrites has important functional implications for the information processing capacities of cortical pyramidal cells and specifically for the interactions between cortical regions. The focus of this article is thus the high-level, computational, implications of the neuro-physiological data concerning dendritic integration. Hence, rather than review the low-level, biophysical, properties and mechanisms of dendritic integration this article concentrates on the abstract, functional, principles that can be derived from this data. These computational properties are illustrated by several connectionist models which are reviewed.

2 Physiology

It is an implicit assumption for nearly all connectionist models that dendritic morphology is irrelevant to neuronal function (Mel, 1999). Hence, all inputs to a model neuron are treated equally and a single integration function, such as the sum of pre-synaptic activities weighted by the synaptic strengths, operates over all inputs. Such models, at most, acknowledge that dendrites have a structural role, such as increasing the receptive surface area of the neuron, but do not accept that dendrites play any role in information processing (Mel, 1999). However, in biological neurons, dendritic morphology and the locations of synapses within the dendritic arbor, are not only related to connectivity but are likely to have functional importance (Fiala and Harris, 1999; Spruston et al., 1994). Non-linear operations are performed by multiple, functionally distinct, dendritic subunits before integration at the soma (Häusser, 2001; Häusser et al., 2000; Koch and Segev, 2000; Mel, 1994, 1999; Segev, 1995; Segev and Rall, 1998). It is thus not unreasonable to assume that at a larger scale the distal (*i.e.*, apical) and proximal (mainly basal) dendrites of pyramidal cells act as separate dendritic compartments (Yuste et al., 1994). Indeed, direct physiological evidence does suggest that the apical dendrite acts as a separate compartment since activation applied to the apical dendrites (of pyramidal cells in layer V) is integrated prior to transmission to the soma (Körding and König, 2000b, 2001b; Larkum et al., 1999).

The anatomically observed segregation of input sources, between apical and basal dendrites, may thus have functional significance. The axon initial segment acts as the final site of integration as it is here that action potential initialization occurs (Stuart et al., 1997b). However, inputs to different dendritic regions may contribute to this output in different ways (Larkum et al., 2001). Inputs at the apical dendrite cause smaller, but more protracted, excitatory post-synaptic potentials (EPSPs) at the soma than do inputs applied to the basal dendrites (Budd, 1998; Rockland, 1998). Hence, apical inputs have weaker effects on output activity than basal inputs. Such findings are consistent with the suggestion that feedback acts to modulate responses that are primarily driven by afferent inputs (Crick and Koch, 1998; Friston and Büchel, 2000; Koch and Segev, 2000). Hence, in contrast to most connectionist models, physiological evidence suggests that inputs to the different dendritic arbors of pyramidal cells are not treated homogeneously.

3 Computation

A neuron in which different sets of inputs can be integrated separately has the potential to operate in a variety of ways which are not possible for the conventional model of a neuron in which all inputs are treated equally. Each compartment might implement a different integration function or a different learning rule. Furthermore, each compartment may have a different effect on the activity of the node, or on learning. This section explores these computational implications by reviewing several connectionist models that have employed neurons with separate apical and basal compartments. Consideration is also made of other models which require distinct sources of information to be treated differently and which could thus be directly implemented using neurons with separate apical and basal compartments.

Most models simulate perceptual tasks and consequently could be interpreted as models of pyramidal cells in the superficial layers of sensory regions. For such neurons sensory-driven, feedforward, information is applied to the basal dendrite while top-down, feedback, information arrives at the apical dendrites. Therefore, where appropriate, “feedforward” and “feedback” will be used as shorthand for basal and apical

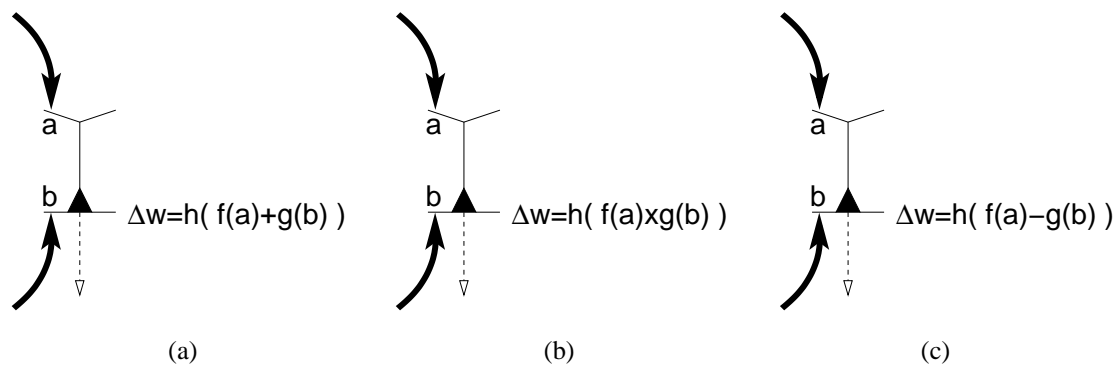


Figure 3: Illustrations of three possible ways in which the stimulation ('a' or 'b') received by each dendrite could affect learning of synaptic weights ('w'). The functions 'f', 'g' and 'h' could potentially take numerous alternative forms. Various functions (both linear and nonlinear) have been employed in different models. Weight changes are also likely to depend on the pre-synaptic activity at each individual synapse. Note that a different learning rule could be used to adjust the synaptic weights of each dendrite.

inputs respectively.

3.1 Learning

3.1.1 Correlated-Activity-Driven Learning

Feedback to the apical dendrite might be used to modify learning in the basal dendrite so as to refine the receptive fields of nodes (Rolls and Treves, 1998). Apical inputs could thus act to coordinate learning between regions. Even when learning is unsupervised, the apical inputs to a particular region can be interpreted as providing supervision, reinforcement, or bias for learning appropriate representations at the basal synapses. Several models have used this approach (Körding and König, 2000b,c,d, 2001a; Ryder and Favorov, 2001; Spratling, 1999). In these models, the principal aim is for feedback information to influence learning (and hence the future response properties of the node) rather than the current neural activity. Hence, the node output is generally determined by the activation received by the basal dendrite only (Körding and König, 2000b,c,d; Spratling, 1999) and the apical input is correlated with the required response to the current sensory stimulus. Strong apical input should thus modify learning so as to bias the node towards representing the current basal inputs. There are many possible learning rules that can achieve this aim. One straightforward approach is to allow only the node with the highest apical input to adjust its basal weights (Körding and König, 2001a) or to allow learning in all those nodes for which the apical input exceeds a threshold (Körding and König, 2000d) or for which the total activation in the apical and basal dendrites exceeds a threshold (Körding and König, 2000b), as illustrated in Figure 3(a). These models have been used to demonstrate that by using a variety of activation functions and learning rules a neural network, in which nodes have two functionally distinct dendrites, can successfully learn a variety of tasks (Körding and König, 2000b, 2001a). These tasks require nodes to learn correlations between separate information streams. The utility of such learning has been noted previously, and many other connectionist algorithms have been applied to similar tasks (Balkenius, 1995; Becker, 1996; Becker and Hinton, 1992; de Sa, 1994; de Sa and Ballard, 1998; Der and Smyth, 1998; Eglén et al., 1997; Kay and Phillips, 1997; Phillips et al., 1995; Phillips and Singer, 1997). However, in such algorithms nodes are required to have access to non-locally available information, or to have separate sets of connections from each information stream. Such models can thus be implemented naturally using a network in which nodes have two dendritic processes (Körding and König, 2001a).

In the models described above, the strength of the activation received by the apical dendrite serves to gate learning. Rather than using the apical input to turn learning on or off, the strength of the apical activation can be used to directly scale the magnitude of the synaptic weight changes (Spratling, 1999), as illustrated in Figure 3(b). Activity-dependent learning is then a tripartite function of pre-synaptic activity

and the post-synaptic activity of both dendrites. In this case, the stronger the apical input, the more the basal weights are modified. Furthermore, weak apical input can change the sign of learning and cause the node to move its receptive field away from the current stimulus. The same learning rule is used to adjust synaptic weights on the apical dendrite, so that learning at the apical synapses is modulated by the strength of activation at the basal dendrites (Spratling, 1999). Apical and basal synapses learn strong weights to input patterns which are correlated across the two input streams. This algorithm has been used for simple perceptual learning tasks in which classification of stimuli applied to the basal dendrite is guided by contextual or supervisory signals applied to the apical dendrite. Apical input has also been used as a source of reinforcement for learning a simple behavioral task (Spratling, 1999).

In order for synaptic weight changes in one dendrite to be effected by the activation received at a second dendrite it is necessary for there to be a mechanism by which the second dendrite can communicate information about its activity to the other dendrite. Dendritically generated calcium spikes can be initiated by strong synchronous synaptic activation of the apical dendrite (Häusser et al., 2000). These calcium spikes propagate towards the soma (Häusser et al., 2000) and have been proposed as triggers for learning events (Körding and König, 2000b,d, 2001a). However, calcium spikes also have an effect on the activity of the cell, typically causing bursts of action potentials (Larkum et al., 1999; Stuart et al., 1997a). The output activity of the cell is an alternative mechanism through which each dendrite could influence learning in the other dendrite. Ryder and Favorov (2001) present such a model. The activity in both dendrites contributes equally to the final output of the node and the magnitude of this output is used by each dendrite (along with its own activity level) to determine the strength of learning. For any form of activity-dependent learning, it is necessary for the synapses to receive information about the post-synaptic activity of the cell (Magee and Johnston, 1997; Stuart and Häusser, 2001). Action potentials initiated at the axon initial segment not only travel outwards, along the axon, but also propagate back into the soma and dendrites (Häusser et al., 2000; Koch and Segev, 2000). The propagation of axonally initiated action potentials back into the dendritic tree is likely to provide information about the post-synaptic activity level of the cell which can influence synaptic plasticity (Häusser et al., 2000; Magee and Johnston, 1997; Stuart and Häusser, 2001; Stuart et al., 1997b). Furthermore, the coincidence of back-propagating post-synaptic action potentials and synaptically generated EPSPs is correlated with the induction of long-term potentiation or long-term depression depending on the relative timing (Häusser et al., 2000; Körding and König, 2000a; Markram et al., 1997; Sánchez-Montañés et al., 2000).

3.1.2 Error-Driven Learning

In the above discussion, apical inputs have been described as providing ‘supervision’ for learning at the basal dendrites. Supervised learning is more commonly associated with error-driven learning, in which weight modifications depend on the difference between the actual output of a node and its required output. Such learning thus depends on the node not only receiving information about the current stimulus but also receiving either error information, or information about the desired activity of the node from which the error can be calculated locally (O’Reilly, 1996, 1998). Such an algorithm can thus be implemented naturally using neurons with two functionally distinct dendrites (Körding and König, 2001a,b; Ryder and Favorov, 2001), as illustrated in Figure 3(c). In contrast, a mechanism to enable conventional, one-dendrite, neurons to perform error-driven learning (O’Reilly, 1998) relies on a complicated mechanisms in which different information is transmitted to the node at different times. A similar mechanism of interleaving information, in order to allow a conventional neuron to segregate data from different sources, has also been found necessary in other learning algorithms (Dayan and Hinton, 1996; Hinton et al., 1995; Hinton and Ghahramani, 1997).

3.2 Activation

In addition to modifying the response properties of neurons in the long-term, through learning, apical inputs are also likely to affect on-going information processing in the short-term by directly influencing neural activity. Apical inputs could thus act to coordinate activity between regions, and hence enable collaborative or interactive information processing. There are many ways in which information arriving from two different sources could be combined to determine the output of a neuron. Existing models generally fall into three classes (Robert, 1999):

1992). One role that has been suggested is for the basal dendrite to receive inputs from the local region while the apical dendrite receives associative inputs from other cortical areas (Levy et al., 1999). In order that memories can be encoded across an arbitrary number of areas, the activity received by the apical dendrite is thresholded, so that the strength of associative input is independent of the number of areas involved in the cell assembly (Levy et al., 1999). A similar approach suggests that nodes should be sensitive to conjunctions of sensory inputs but to disjunctions of inputs from other cells within the assembly (Möller and Groß, 1994, 1995). Such nodes will thus be selective to a particular pattern of input values but can take part in many different cell assemblies. This model is unusual in identifying the apical dendrites as the receptive surface for sensory inputs while the basal dendrites receive internally generated hypotheses or predictions. Each dendrite employs a different learning rule in order to learn conjunctions or disjunctions across their respective inputs (Möller and Groß, 1994, 1995). Hetherington and Shapiro (1993) also found it necessary to use different learning rules for sensory inputs and for the interconnections between cells in the assembly. To ensure that activity within the cell assembly did not spread to other nodes it was necessary to use a learning rule that reduced synaptic weights when there was post-synaptic activity in the absence of pre-synaptic activity. However, since the cell assembly can be active in the absence of the sensory stimulus, such a learning rule could not be used for modifying the connections from the sensory inputs since this could lead to those connections being severed (Hetherington and Shapiro, 1993).

3.2.2 Perception

Top-down effects have been demonstrated to play a crucial role in sensory information processing (Siegel et al., 2000). During visual perception, information is transferred from more peripheral cortical areas to more central areas. In addition to this feedforward propagation of information through the visual hierarchy, feedback connections simultaneously transmit information in the reverse direction and lateral connections integrate information across the visual field (Lamme and Roelfsema, 2000; Lamme et al., 1998). Feedback connections are thus likely to play a prominent role in perception.

Attention is a top-down process that operates via cortical feedback projections (Desimone and Duncan, 1995; Schroeder et al., 2001) targeting the apical dendrites in layer I (Cauller, 1995; Olson et al., 2001). By manipulating attention or expectation, it is possible to explore the effects of feedback on the response properties of cortical pyramidal cells. Attention modulates the sensory-driven activation of cells (Kanwisher and Wojciulik, 2000; Kastner et al., 1999; Luck et al., 1997; McAdams and Maunsell, 2000), such that activity in response to an attended stimulus is increased in amplitude and duration (Kastner and Ungerleider, 2000; Schroeder et al., 2001). Such top-down modulation also affects the on-going competition between cells (Itti and Koch, 2001; Luck et al., 1997; Reynolds et al., 1999). Competition can be biased both by stimulus saliency and by attention (De Weerd et al., 1999; Kastner and Ungerleider, 2000; Olson, 2001). Hence, increased attention has effects similar to increasing the contrast or saliency of the stimulus (Itti and Koch, 2001; Kastner and Ungerleider, 2000; Olson, 2001; Reynolds et al., 2000). Feedback thus serves “to amplify and focus activity” (Hupé et al., 1998). Similar effects of feedback, or recurrent, activity can also be observed in the absence of attention (Lamme and Roelfsema, 2000; Lamme et al., 1998; Lee et al., 1998; Zipser et al., 1996). In the absence of a stimulus, attention increases the rate of spontaneous firing (Kanwisher and Wojciulik, 2000; Kastner et al., 1999; Kastner and Ungerleider, 2000; Luck et al., 1997). Feedback causes weaker EPSPs than feedforward input (Budd, 1998; Shao and Burkhalter, 1996), but can raise the potential of the cell nearer to threshold so that it responds more quickly, and more strongly, to feedforward input.

All connectionist models of perception investigate how feedforward, sensory-driven, information is processed and represented. However, relatively few models have investigated the role of feedback. Even models of perceptual processes, such as attention, in which feedback is known to play a prominent role often do not explicitly include feedback connections (*e.g.*, Itti and Koch, 2001; Koch and Ullman, 1985; Lee et al., 1999; Reynolds et al., 1999). However, as outlined in the previous paragraph, there is a great deal of physiological data that could be used to inform and constrain models which do incorporate feedback. One such model (Grossberg and Raizada, 2000) uses a complex feedback mechanism, involving several cortical layers, to generate widespread inhibition together with more focused excitation. At attended locations, top-down excitation is counterbalanced by top-down inhibition, while at non-attended locations there is net inhibition. The result is that attention alone cannot cause activation of neurons but it can cause relative enhancement of sensory-driven processing. Equivalent modulatory effects could also be achieved

by employing neurons that have two functionally distinct dendrites. In other models (*e.g.*, Olshausen et al., 1993), attention is used to multiplicatively modulate the synaptic strengths of intra-cortical connections so that attended information can be selectively routed to higher cortical regions. Equivalent results can be achieved by using attention to modulate the activity of neurons rather than weights of synapses (Salinas and Abbott, 1997; Salinas and Thier, 2000). Such a model could be implemented in a biologically plausible manner using nodes with two dendrites interacting as illustrated in Figure 4(b).

Modulatory affects on neural activity have also been observed in parietal areas (Andersen et al., 1985; Brotchie et al., 1995) and have been proposed as a common computational mechanism employed throughout the cortex (Phillips and Singer, 1997; Salinas and Sejnowski, 2001; Salinas and Thier, 2000). This mechanism has been modeled by allowing the activity generated by stimulation of the receptive field to be multiplicatively modulated by the response to a separate set of inputs applied to the “gain field” (Salinas and Abbott, 1996; Salinas and Sejnowski, 2001; Salinas and Thier, 2000). An alternative algorithm uses a more complex formula to allow stimulation of a “contextual field” to modulate activity generated at the receptive field (Phillips et al., 1995; Phillips and Singer, 1997). As with models of attention these algorithms require inputs from different sources to have dissimilar effects on activity. Hence, such models could also be naturally implemented using nodes with functionally distinct apical and basal dendritic compartments.

4 Conclusions

Increasing attention is being paid to understanding how dendrites contribute to information processing in single neurons (Häusser et al., 2000; Stuart et al., 1999). Rather than being passive receptive surfaces for synaptic contacts, dendrites perform complex computational functions (Mel, 1994). Related synapses cluster together within the dendritic tree so that local operations are performed by multiple, functionally distinct, dendritic subunits before integration at the soma (Häusser, 2001; Häusser et al., 2000; Koch and Segev, 2000; Mel, 1993; Segev, 1995; Segev and Rall, 1998). The presence of multiple dendritic subunits significantly enhances the computational power of an individual neuron (Mel, 1993, 1994, 1999; Shepherd and Brayton, 1987) and several artificial neural network algorithms have been inspired by this insight (Durbin and Rumelhart, 1989; Mel and Koch, 1990; Rumelhart et al., 1986; Spratling and Hayes, 2000). However, in common with other conventional neural networks which assume dendrites have passive, linear, properties, these models also treat all inputs homogeneously. This review has considered a different way in which dendrites may contribute to the computational properties of neurons: by enabling different sets of synaptic inputs to have distinct functional roles. In such a neuron different sets of inputs can be integrated separately, using the same or different integration functions. The resulting dendritic activities may have differing effects on the activity of the neuron and on learning. Such properties give functional significance to the anatomically observed segregation, between the apical and basal dendrites of pyramidal cells, of axon projections originating in different cortical regions.

Compared with conventional neural networks, an implementation of a model in which neurons have functionally distinct apical and basal dendrites requires only a small increase in computational complexity. However, it results in a model which has the potential to operate in a variety of ways which are not possible for conventional neural networks. Hence, the incorporation of additional neuro-biological mechanisms into connectionist models results in enhanced computational abilities. Furthermore, these models can implement a larger class of connectionist algorithms, and theoretical models, in a biologically plausible manner (Körding and König, 2001a,b). While such flexibility is appealing from a computational stand-point it creates a challenge in finding those mechanisms which are actually used in the cerebral cortex. A large volume of experimental data records the effects of feedforward and feedback activity on the responses of single-cells. Such data could provide strong constraints on models. Feedback modulates activity generated by feedforward processing. Such modulation may play a role in tasks such as recall, priming and attention (Rolls and Treves, 1998). In addition, by influencing activation each dendrite can affect learning in a biologically plausible manner. Neurons are likely to learn correlations between the separate information streams targeting the apical and basal dendrites. Apical inputs can therefore influence learning at the basal dendrite and may be considered a source of reinforcement or supervision. This interpretation is bolstered by the fact that the apical dendrites in layer I not only receive projections from other cortical regions but are also targeted by the limbic system; a widely projecting set of interconnected brain structures concerned with emotion and memory.

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References

- Andersen, R. A., Essick, G. K., and Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science*, 230(4724):456–8.
- Balkenius, C. (1995). Multi-modal sensing for robot control. In Niklasson, L. F. and Bodén, M. B., editors, *Current trends in connectionism*, pages 203–16. Lawrence Erlbaum, Hillsdale, NJ.
- Barbas, H. and Rempel-Clower, N. (1997). Cortical structure predicts the pattern of corticocortical connections. *Cerebral Cortex*, 7:635–46.
- Barlow, H. B. (1994). What is the computational goal of the neocortex? In Koch, C. and Davis, J. L., editors, *Large-Scale Neuronal Theories of the Brain*, chapter 1. MIT Press, Cambridge, MA.
- Becker, S. (1996). Mutual information maximization: models of cortical self-organization. *Network: Computation in Neural Systems*, 7:7–31.
- Becker, S. and Hinton, G. E. (1992). A self-organizing neural network that discovers surfaces in random-dot stereograms. *Nature*, 355(6356):161–3.
- Braitenberg, V. (1978). Cortical architectonics: general and areal. In Brazier, M. A. B. and Petsche, H., editors, *Architectonics of the Cerebral Cortex*, pages 443–65. Raven Press, New York, NY.
- Brotchie, P. R., Andersen, R. A., Snyder, L. H., and Goodman, S. J. (1995). Head position signals used by parietal neurons to encode locations of visual stimuli. *Nature*, 375(6528):232–5.
- Budd, J. M. L. (1998). Extrastriate feedback to primary visual cortex in primates: a quantitative analysis of connectivity. *Proceedings of the Royal Society of London. Series B*, 265(1400):1037–44.
- Cauler, L. J. (1995). Layer I of primary sensory neocortex: where top-down converges upon bottom-up. *Behavioural Brain Research*, 71(1-2):163–70.
- Crick, F. and Asanuma, C. (1986). Certain aspects of the anatomy and physiology of the cerebral cortex. In Rumelhart, D. E., McClelland, J. L., and The PDP Research Group, editors, *Parallel Distributed Processing: Explorations in the Microstructures of Cognition. Volume 2: Psychological and Biological Models*, pages 333–71. MIT Press, Cambridge, MA.
- Crick, F. and Koch, C. (1998). Constraints on cortical and thalamic projections: the no-strong-loops hypothesis. *Nature*, 391:245–50.
- Dayan, P. and Hinton, G. E. (1996). Varieties of helmholtz machine. *Neural Networks*, 9(8):1385–403.
- de Sa, V. R. (1994). Learning classification with unlabeled data. In Cowan, J. D., Tesauero, G., and Al-spector, J., editors, *Advances in Neural Information Processing Systems 6*, pages 112–9, San Francisco. Morgan Kaufmann.
- de Sa, V. R. and Ballard, D. (1998). Category learning through multi-modality sensing. *Neural Computation*, 10(5):1097–117.
- De Weerd, P., Peralta, M. R., Desimone, R., and Ungerleider, L. G. (1999). Loss of attentional stimulus selection after extrastriate cortical lesions in macaques. *Nature Neuroscience*, 2(8):753–8.
- Der, R. and Smyth, D. (1998). Local online learning of coherent information. *Neural Networks*, 11(5):909–25.
- Desimone, R. and Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18:193–222.
- Durbin, R. and Rumelhart, D. E. (1989). Product units: a computationally powerful and biologically plausible extension to backpropagation networks. *Neural Computation*, 1:133–42.
- Ebdon, M. (1996). *Towards a General Theory of Cerebral Neocortex*. PhD thesis, University of Sussex.
- Eglen, S., Bray, A., and Stone, J. (1997). Unsupervised discovery of invariances. *Network: Computation in Neural Systems*, 8(4):441–52.
- Felleman, D. J. and Van Essen, D. C. (1991). Distributed hierarchical processing in primate cerebral cortex. *Cerebral Cortex*, 1:1–47.
- Fiala, J. and Harris, K. (1999). Dendritic structure and spines. In Stuart, G., Spruston, N., and Häusser, M., editors, *Dendrites*, chapter 1, pages 1–34. Oxford University Press, Oxford, UK.

- Friston, K. J. and Büchel, C. (2000). Attentional modulations of effective connectivity from V2 to V5/MT in humans. *Proceedings of the National Academy of Science USA*, 97(13):7591–6.
- Fukushima, K. (1987). Neural network model for selective attention in visual pattern recognition and associative recall. *Applied Optics*, 26(23):4985–92.
- Grossberg, S. and Raizada, R. (2000). Contrast-sensitive perceptual grouping and object-based attention in the laminar circuits of primary visual cortex. *Vision Research*, 40(10-12):1413–32.
- Häusser, M. (2001). Synaptic function: dendritic democracy. *Current Biology*, 11(1):R10–2.
- Häusser, M., Spruston, N., and Stuart, G. J. (2000). Diversity and dynamics of dendritic signalling. *Science*, 290(5492):739–44.
- Hebb, D. O. (1949). *The Organization of Behavior: A Neuropsychological Theory*. Wiley.
- Hetherington, P. A. and Shapiro, M. L. (1993). Simulating Hebb cell assemblies: the necessity for partitioned dendritic trees and a post-not-pre LTD rule. *Network: Computation in Neural Systems*, 4:135–53.
- Hinton, G. E., Dayan, P., Frey, B. J., and Neal, R. M. (1995). The wake-sleep algorithm for unsupervised neural networks. *Science*, 268(5214):1158–61.
- Hinton, G. E. and Ghahramani, Z. (1997). Generative models for discovering sparse distributed representations. *Philosophical Transactions of the Royal Society of London. Series B*, 352(1358):1177–90.
- Hopfield, J. (1982). Neural networks and physical systems with emergent collective computational abilities. *Proceedings of the National Academy of Science USA*, 79(8):2554–8.
- Hupé, J. M., James, A. C., Payne, B. R., Lomber, S. G., Girard, P., and Bullier, J. (1998). Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. *Nature*, 394(6695):784–7.
- Itti, L. and Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, 2(3):194–202.
- Johnson, R. R. and Burkhalter, A. (1997). A polysynaptic feedback circuit in rat visual cortex. *Journal of Neuroscience*, 17(18):7129–40.
- Kanwisher, N. and Wojciulik, E. (2000). Visual attention: insights from brain imaging. *Nature Reviews Neuroscience*, 1(2):91–100.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., and Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, 22(4):751–61.
- Kastner, S. and Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, 23:315–41.
- Kay, J. and Phillips, W. A. (1997). Activation functions, computational goals and learning rules for local processors with contextual guidance. *Neural Computation*, 9(4):895–910.
- Koch, C. and Segev, I. (2000). The role of single neurons in information processing. *Nature Neuroscience*, 3(supplement):1171–7.
- Koch, C. and Ullman, S. (1985). Shifts in selective visual attention: towards the underlying neural circuitry. *Human Neurobiology*, 4(4):219–27.
- Koerner, E., Tsujino, H., and Masutani, T. (1997). A cortical-type modular neural network for hypothetical reasoning. *Neural Networks*, 10(5):791–814.
- Kohonen, T. (1972). Correlation matrix memories. *IEEE Transactions on Computers*, 21:353–9.
- Körding, K. P. and König, P. (2000a). A learning rule for dynamic recruitment and decorrelation. *Neural Networks*, 13(1):1–9.
- Körding, K. P. and König, P. (2000b). Learning with two sites of synaptic integration. *Network: Computation in Neural Systems*, 11(1):25–39.
- Körding, K. P. and König, P. (2000c). A spike based learning rule for generation of invariant representations. *Journal of Physiology (Paris)*, 94(5–6):539–48.
- Körding, K. P. and König, P. (2000d). Two sites of synaptic integration: relevant for learning. In *International Joint Conference on Neural Networks*. IEEE Computer Society.
- Körding, K. P. and König, P. (2001a). Neurons with two sites of synaptic integration learn invariant representations. *Neural Computation*, 13(12):2823–49.
- Körding, K. P. and König, P. (2001b). Supervised and unsupervised learning with two sites of synaptic integration. *Journal of Computational Neuroscience*, 11(3):207–15.
- Lamme, V. A. F. and Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, 23(11):571–9.

- Lamme, V. A. F., Supèr, H., and Spekreijse, H. (1998). Feedforward, horizontal, and feedback processing in the visual cortex. *Current Opinion in Neurobiology*, 8(4):529–35.
- Larkum, M. E., Zhu, J. J., and Sakmann, B. (1999). A new cellular mechanism for coupling inputs arriving at different cortical layers. *Nature*, 398(6725):338–41.
- Larkum, M. E., Zhu, J. J., and Sakmann, B. (2001). Dendritic mechanisms underlying the coupling of the dendritic with the axonal action potential initiation zone of adult rat layer 5 pyramidal neurons. *Journal of Physiology*, 533(2):447–66.
- Lee, D. K., Itti, L., Koch, C., and Braun, J. (1999). Attention activates winner-take-all competition among visual filters. *Nature Neuroscience*, 2(4):375–81.
- Lee, T. S., Mumford, D., Romero, R., and Lamme, V. A. F. (1998). The role of primary visual cortex in higher level vision. *Vision Research*, 38:2429–54.
- Levy, N., Horn, D., and Ruppín, E. (1999). Associative memory in a multimodular network. *Neural Computation*, 11:1717–37.
- Luck, S. J., Chelazzi, L., Hillyard, S. A., and Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, 77:24–42.
- Magee, J. C. and Johnston, D. (1997). A synaptically controlled, associative signal for Hebbian plasticity in hippocampal neurons. *Science*, 275(5297):209–13.
- Markram, H., Lubke, J., Frotscher, M., and Sakmann, B. (1997). Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. *Science*, 275(5297):213–5.
- McAdams, C. J. and Maunsell, J. H. R. (2000). Attention to both space and feature modulates neuronal responses in macaque area V4. *Journal of Neurophysiology*, 83(3):1751–5.
- McClelland, J. L. and Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception, part 1: an account of basic findings. *Psychological Review*, 88:375–407.
- Mel, B. W. (1993). Synaptic integration in an excitable dendritic tree. *Journal of Neurophysiology*, 70(3):1086–101.
- Mel, B. W. (1994). Information processing in dendritic trees. *Neural Computation*, 6:1031–85.
- Mel, B. W. (1999). Why have dendrites? A computational perspective. In Stuart, G., Spruston, N., and Häusser, M., editors, *Dendrites*, chapter 11, pages 271–89. Oxford University Press, Oxford, UK.
- Mel, B. W. and Koch, C. (1990). Sigma-pi learning: on radial basis functions and cortical associative learning. In Touretzky, D. S., editor, *Advances in Neural Information Processing Systems 2*, pages 474–81, San Francisco. Morgan Kaufmann.
- Miller, R. (1996). Neural assemblies and laminar interactions in the cerebral cortex. *Biological Cybernetics*, 75:253–61.
- Möller, R. and Groß, H.-M. (1994). Perception through anticipation. In *Proceedings of PerAc '94 – From Perception to Action*, pages 408–11, Los Alamitos, CA. IEEE Computer Society Press.
- Möller, R. and Groß, H.-M. (1995). Possible functional roles of bipartite dendrites of pyramidal cells. In *Proceedings of the Third Annual SNN Symposium on Neural Networks*, pages 51–4. Springer-Verlag.
- Mountcastle, V. B. (1998). *Perceptual Neuroscience: The Cerebral Cortex*. Harvard University Press, Cambridge, MA.
- Mumford, D. (1992). On the computational architecture of the neocortex II: the role of cortico-cortical loops. *Biological Cybernetics*, 66:241–51.
- Mumford, D. (1994). Neuronal architectures for pattern-theoretic problems. In Koch, C. and Davis, J. L., editors, *Large-Scale Neuronal Theories of the Brain*, pages 125–52. MIT Press, Cambridge, MA.
- Olshausen, B. A., Anderson, C. H., and Van Essen, D. C. (1993). A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. *The Journal of Neuroscience*, 13(11):4700–19.
- Olson, C. R. (2001). Object-based vision and attention in primates. *Current Opinion in Neurobiology*, 11(2):171–9.
- Olson, I. R., Chun, M. M., and Allison, T. (2001). The contextual guidance of attention: human intracranial event-related potential evidence for feedback modulation in anatomically early temporally late stages of visual processing. *Brain*, 124(7):1417–25.
- O'Reilly, R. C. (1996). Biologically plausible error-driven learning using local activation differences: the generalized recirculation algorithm. *Neural Computation*, 8(5):895–938.
- O'Reilly, R. C. (1998). Six principles for biologically based computational models of cortical cognition. *Trends in Cognitive Sciences*, 2(11):455–62.

- Paré, D., Lang, E. J., and Destexhe, A. (1998). Inhibitory control of somatodendritic interactions underlying action potentials in neocortical pyramidal neurons in vivo: an intracellular and computational study. *Neuroscience*, 84(2):377–402.
- Phillips, W. A., Kay, J., and Smyth, D. (1995). The discovery of structure by multi-stream networks of local processors with contextual guidance. *Network: Computation in Neural Systems*, 6(2):225–46.
- Phillips, W. A. and Singer, W. (1997). In search of common foundations for cortical computation. *Behavioural and Brain Sciences*, 20(4):657–722.
- Rao, R. P. N. (1999). An optimal estimation approach to visual perception and learning. *Vision Research*, 39(11):1963–89.
- Rao, R. P. N. and Ballard, D. H. (1997). Dynamical model of visual recognition predicts neural response properties in the visual cortex. *Neural Computation*, 9(4):721–63.
- Rao, R. P. N. and Ballard, D. H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2(1):79–87.
- Reynolds, J. H., Chelazzi, L., and Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *Journal of Neuroscience*, 19:1736–53.
- Reynolds, J. H., Pasternak, T., and Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron*, 26:703–14.
- Robert, A. (1999). *Lamination and Within-Area Integration in the Neocortex*. PhD thesis, University of California, San Diego.
- Rockland, K. S. (1998). Complex microstructures of sensory cortical connections. *Current Opinion in Neurobiology*, 8:545–51.
- Rolls, R. T. and Treves, A. (1998). *Neural Networks and Brain Function*. Oxford University Press, Oxford, UK.
- Rumelhart, D. E., McClelland, J. L., and The PDP Research Group, editors (1986). *Parallel Distributed Processing: Explorations in the Microstructures of Cognition. Volume 1: Foundations*. MIT Press, Cambridge, MA.
- Ryder, D. and Favorov, O. (2001). The new associationism: a neural explanation for the predictive powers of the cerebral cortex. *Brain and Mind*, 2(2):161–94.
- Salinas, E. and Abbott, L. F. (1996). A model of multiplicative neural responses in parietal cortex. *Proceedings of the National Academy of Science USA*, 93:11956–61.
- Salinas, E. and Abbott, L. F. (1997). Invariant visual perception from attentional gain fields. *Journal of Neurophysiology*, 77(6):3267–72.
- Salinas, E. and Sejnowski, T. J. (2001). Gain modulation in the central nervous system: where behavior, neurophysiology and computation meet. *The Neuroscientist*, 7(5):430–40.
- Salinas, E. and Thier, P. (2000). Gain modulation: a major computational principle of the central nervous system. *Neuron*, 27:15–21.
- Sánchez-Montañés, M. A., Verschure, P. F. M. J., and König, P. (2000). Local and global gating of synaptic plasticity. *Neural Computation*, 12(3):519–29.
- Schroeder, C. E., Mehta, A. D., and Foxe, J. J. (2001). Determinants of attentional control in cortical processing: evidence from human and monkey electrophysiologic investigations. *Frontiers in Bioscience*, 6:d672–84.
- Segev, I. (1995). Dendritic processing. In Arbib, M. A., editor, *The Handbook of Brain Theory and Neural Networks*, pages 282–9. MIT Press, Cambridge, MA.
- Segev, I. and Rall, W. (1998). Excitable dendrites and spines: earlier theoretical insights elucidate recent direct observations. *Trends in Neurosciences*, 21(11):453–60.
- Shao, Z. and Burkhalter, A. (1996). Different balance of excitation and inhibition in forward and feedback circuits of rat visual cortex. *Journal of Neuroscience*, 16(22):7353–65.
- Shepherd, G. M. and Brayton, R. K. (1987). Logic operations are properties of computer-simulated interactions between excitable dendritic spines. *Neuroscience*, 21:151–66.
- Siegel, M., Kording, K. P., and König, P. (2000). Integrating top-down and bottom-up sensory processing by somato-dendritic interactions. *Journal of Computational Neuroscience*, 8:161–73.
- Spratling, M. W. (1999). *Artificial Ontogenesis: A Connectionist Model of Development*. PhD thesis, University of Edinburgh.
- Spratling, M. W. and Hayes, G. M. (2000). Learning synaptic clusters for non-linear dendritic processing. *Neural Processing Letters*, 11(1):17–27.

- Spruston, N., Jaffe, D. B., and Johnston, D. (1994). Dendritic attenuation of synaptic potentials and currents: the role of passive membrane properties. *Trends in Neuroscience*, 17:161–6.
- Stuart, G. and Häusser, M. (2001). Dendritic coincidence detection of EPSPs and action potentials. *Nature Neuroscience*, 4(1):63–71.
- Stuart, G., Schiller, J., and Sakmann, B. (1997a). Action potential initiation and propagation in rat neocortical pyramidal neurons. *The Journal of Physiology*, 505(3):617–32.
- Stuart, G., Spruston, N., and Häusser, M., editors (1999). *Dendrites*. Oxford University Press, Oxford, UK.
- Stuart, G., Spruston, N., Sakmann, B., and Häusser, M. (1997b). Action potential initiation and backpropagation in neurons of the mammalian CNS. *Trends in Neurosciences*, 20(3):125–31.
- Wickelgren, W. A. (1992). Webs, cell assemblies, and chunking in neural nets. *Concepts in Neuroscience*, 3(1):1–53.
- Willshaw, D. J., Longuet-Higgins, H. C., and Buneman, O. P. (1969). Non-holographic associative memories. *Nature*, 222(197):960–2.
- Yuste, R., Gutnick, M. J., Saar, D., Delaney, K. R., and Tank, D. W. (1994). Ca^{2+} accumulations in dendrites of neocortical pyramidal neurons: an apical band and evidence for two functional compartments. *Neuron*, 13:23–43.
- Zipser, K., Lamme, V. A. F., and Schiller, P. H. (1996). Contextual modulation in primary visual cortex. *Journal of Neuroscience*, 16(22):7376–89.