

Modeling Directional Selectivity Using Self-Organizing Delay-Adaptation Maps^{*}

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Abstract

Using a delay adaptation learning rule, we model the activity-dependent development of directionally selective cells in the primary visual cortex. Based on input stimuli, a learning rule shifts delays to create synchronous arrival of spikes at cortical cells. As a result, delays become tuned creating a smooth cortical map of direction selectivity. This result demonstrates how delay adaptation can serve as a powerful abstraction for modeling temporal learning in the brain.

Key words: self-organization, delay adaptation, direction selectivity, cortical maps, cortical development, visual cortex

1 Introduction

There has recently been much progress in understanding how the properties of the primary visual cortex (V1) develop based on visual input. There are models that explain the development of orientation columns, ocular dominance columns and spatial frequency organization [3, 20]. There is also a variety of models of directional selectivity in V1 [1, 6, 7, 13, 14, 16]. All of these models are based on networks with fixed, hard-wired delays. As an alternative, models with adapting delays have recently been proposed by several researchers [4, 8, 10, 11]. These networks learn temporal information directly, through learning rules that adapt the delays in the network.

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There are two ways in which delay adaptation can be implemented computationally [5]. In *delay selection* an initial range of delay lines are pruned during development into an appropriate set of delays. In *delay shift* the transmission delays are altered based on the timing of pre- and post-synaptic spikes. [5] showed that delay shift networks are stable and can approximate the behavior of delay selection models with more traditional weight learning rules [9]. One can think of a single delay shift connection to be equivalent to a collection of connections with random fixed delays and a spike-timing dependent weight learning rule.

In this paper, we demonstrate that a delay shift learning rule can serve as a powerful abstraction of how temporal learning could occur in the brain. Prior computational support for this idea includes a recent result of [15], who show how a temporally asymmetric learning rule combined with unreliable transmission times can induce drifts in the axonal and dendritic delays that effectively create a delay adaptation learning rule. It is also possible that something like delay shift is directly computed in the nervous system. Fiala et al. [8] and Steuber and Willshaw [18, 19] gave a low-level explanation of how such learning could occur in cerebellar Purkinje cells based on metabotropic glutamate receptors.

The main goal of our research is to understand the development of directional selectivity in V1. Using a delay shift learning rule, we built a temporal analog to the classic self-organizing map: the self-organizing delay adaptation (SODA) map. The SODA map developed a smoothly changing map of directional selectivity, demonstrating how delay adaptation can serve as a mechanism for temporal learning in the brain.

2 The SODA Map

The SODA map is composed of integrate-and-fire neurons organized into two fully connected layers: a two-dimensional input layer modeling the connections from the retina through LGN, and a two-dimensional computing layer modeling the cortex. Afferent connections from retina to cortex each have the same constant weight, but have a variable, learned delay. In order to create the competition between the cortical neurons that is necessary for them to differentiate and organize, the cortex has short-range excitatory and long-range inhibitory lateral connections, each with the same small constant weight and delay.

Afferent delays are adjusted according to a delay learning rule that depends on the timing of pre- and post-synaptic spikes [4]. For a pre-synaptic spike arriving at time t_{pre} and a post-synaptic neuron that fires at time t_{post} , the

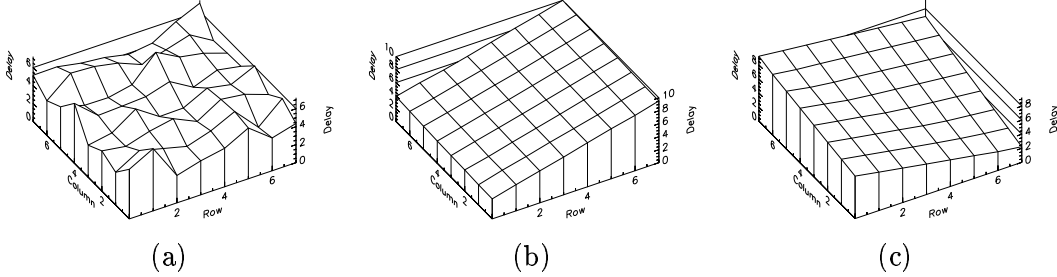


Fig. 1. **Position Delay Tuning** Each figure shows time delays on the connections from each location in the retina to one particular cell in the cortex. (a) Initial tuning. (b) A neuron tuned to motion in one direction (west). This neuron corresponds to position (3,3) on the map in figure 2b. (c) A neuron tuned to two directions of motion (east and south) in position (5,7) in figure 2b.

change in delay, W_τ , is computed as $W_\tau(s) = -s\left(\frac{\exp(-\frac{s^2}{c^2})}{c}\right) - d$, where c is a positive constant, d is a small negative bias and $s = t_{pre} - t_{post}$. As one might intuit, delays are increased for input spikes that arrive early relative to the post-synaptic spike and are decreased for late arrivals. One can think of this learning rule as a temporal analog to Hebb's rule; instead of weights being adjusted to create spatially coincident activation, delays are adjusted to create temporally coincident activation.

3 Simulation and Results

Initially, all afferent delays are randomly assigned from a Gaussian distribution (figure 1a). As a result, the neurons exhibit little selectivity. The small amount of organization that we see in the initial map (figures 1a and 2a) is due entirely to the excitatory lateral connections. During training, the network is repeatedly presented with one of four stimuli, each of which is a bar of activity moving at a constant speed in one of the four cardinal directions.

In this process all of the neuron's delays become tuned and coherent. They form a profile tuned to a particular stimulus such that all of the input spikes from that stimulus will arrive almost coincidentally to the cortical neuron, thus creating maximal firing. Plotting these delays on the retina we see a plane whose slope corresponds to the speed of motion of the input stimulus. Different areas of the map (figure 2b) respond optimally to one or two input stimuli. In addition the map exhibits transitions between different areas.

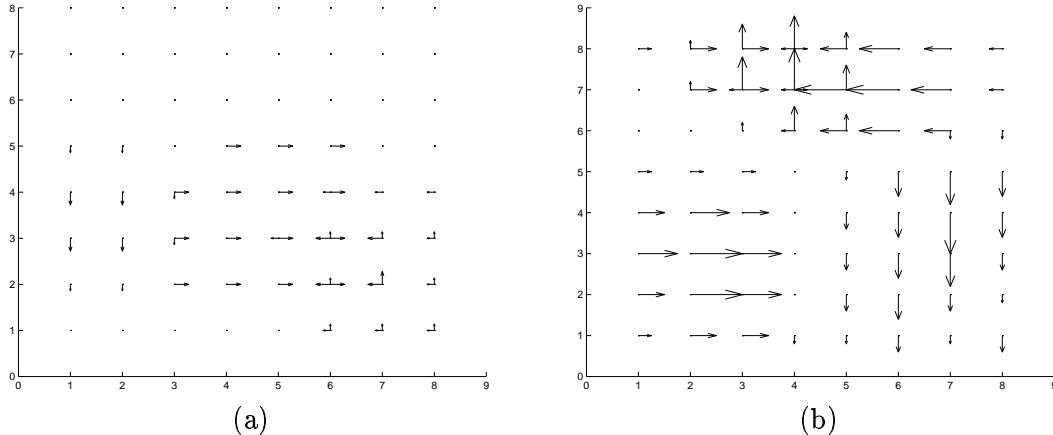


Fig. 2. Directional Selectivity Map The x and y axes indicate location in the cortex. At each location, the response of a cortical neuron in the map is represented. Each arrow represents the strength of that neuron’s response to the stimulus that moves in the arrow’s direction. No arrow means that the neuron has no response to that stimulus. (a) Initially, the map shows very little organization and tuning. (b) After training, we can see that the map has become organized, with different areas likely to respond to one or two of the input stimuli, and smooth transitions between these areas.

4 Discussion and Future Work

We have shown how a self-organizing map using a delay adaptation learning rule develops an organization based on directional selectivity. In our maps, because delays are the only parameters that adapt, direction is the only stimulus property that can be represented and cortical cells tend to be adjacent to other cortical cells with the same directional selectivity. In V1, the pattern of directional selectivity changes in a slow continuous fashion, and then has “fractures” where the directional selectivity shifts abruptly [17, 21]. These fractures are due to the fact that maps of both orientation and directional selectivity are overlaid in the same brain area. The next step in our modeling is to add a weight learning rule to SODA; with both delay and weight learning rules, maps of directional selectivity and orientation will develop together, and we expect the resulting map to exhibit the fractures and pinwheels that develop in the cortex.

Temporal computation is not restricted to the visual system of the mammalian brain. The lateral line system of weakly electric fish, and the auditory system of barn owls and echo-locating bats all depend on precise neuronal time codings [2]. In particular, the auditory cortex forms a map of inter-aural delays in mammals and birds [12]. SODA computation models are ideal tools for understanding how maps of time varying input can be learned.

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References

- [1] B. Blais, L. N. Cooper, and H. Shouval, Formation of direction selectivity in natural scene environments, *Neural Computation* 12 (2000).
- [2] C. E. Carr, Processing of temporal information in the brain, *Annual Review of Neuroscience* 16 (1993) 223–243.
- [3] E. Erwin, K. Obermayer, and K. Schulten, Models of orientation and ocular dominance columns in the visual cortex: A critical comparison, *Neural Computation* 7 (1995) 425–468.
- [4] C. W. Eurich, K. Pawelzik, U. Ernst, J. D. Cowan, and J. G. Milton, Dynamics of self-organized delay adaptation, *Physical Review Letters* 82 (1999) 1594–1597.
- [5] C. W. Eurich, K. Pawelzik, U. Ernst, A. Thiel, J. D. Cowan, and J. G. Milton, Delay adaptation in the nervous system, *Neurocomputing* 32 (2000) 741–748.
- [6] I. Farkas and R. Miikkulainen, Modeling the self-organization of directional selectivity in the primary visual cortex, in: *Proceedings of the Ninth International Conference on Artificial Neural Networks: ICANN-99* (Amsterdam; New York: North-Holland, 1999) In press.
- [7] J. C. Feidler, A. B. Saul, A. Murthy, and A. L. Humphrey, Hebbian learning and the development of direction selectivity: The role of geniculate response timings, *Network – Computation in Neural Systems* 8 (1997) 195–214.
- [8] J. C. Fiala, S. Grossberg, and D. Bullock, Metabotropic glutamate receptor activation in cerebellar purkinje cells as substrate for adaptive timing of the classically conditioned eye-blink response, *Journal of Neuroscience* 16 (1996) 3760–3774.
- [9] W. Gerstner, R. Kempter, J. L. van Hemmen, and H. Wagner, A neuronal learning rule for sub-millisecond temporal coding, *Nature* 383 (1996) 76–78.
- [10] J. J. Hopfield, Pattern recognition computation using action potential timing for stimulus representation, *Nature* 376 (1995) 33–36.
- [11] H. Hünig, H. Glünder, and G. Palm, Synaptic delay learning in pulse-coupled neurons, *Neural Computation* 10 (1998) 555–565.
- [12] E. I. Knudsen, S. du Lac, and S. D. Esterly, Computational maps in the brain, in: W. M. Cowan, E. M. Shooter, C. F. Stevens, and R. F.

- Thompson, eds., *Annual Review of Neuroscience* (Annual Reviews, Palo Alto, 1987) 41–65.
- [13] R. Maex and G. A. Orban, Model circuit of spiking neurons generating directional selectivity in simple cells, *Journal of Neurophysiology* 75 (1996) 1515–1545.
 - [14] T. Nagano and M. Fujiwara, A neural network model for the development of direction selectivity in the visual cortex, *Biological Cybernetics* 32 (1979) 1–8.
 - [15] W. Senn, M. Schneider, and B. Ruf, activity-dependent selection of axonal and dendritic delays or, why synaptic transmission should be unreliable, *Neural Computation* (2001), In press.
 - [16] M. Sereno, *Neural Computation Of Pattern Motion: Modeling Stages Of Motion Analysis In The Primate Visual Cortex* (MIT Press, Cambridge, MA, 1993).
 - [17] A. Shmuel and A. Grinwald, Functional organization for direction of motion and its relationship to orientation maps in cat area 18, *Journal of Neuroscience* 16 (1996) 6945–6964.
 - [18] V. Steuber and D. J. Willshaw, How a single purkinje cell could learn the adaptive timing of the classically conditioned eye-blink response, in: *Proceedings of the Seventh International Conference on Artificial Neural Networks: ICANN-97* (Berlin; New York: Springer-Verlag, 1997) 115–120.
 - [19] V. Steuber and D. J. Willshaw, Adaptive leaky integrator models of cerebellar purkinje cells can learn the clustering of temporal patterns, *Neurocomputing* 26 (1999) 271–276.
 - [20] N. V. Swindale, The development of topography in the visual cortex: A review of models, *Network – Computation in Neural Systems* 7 (1996) 161–247.
 - [21] M. Weliky, W. H. Bosking, and D. Fitzpatrick, A systematic map of direction preference in primary visual cortex, *Nature* 379 (1996) 725–728.