

Can Hebbian Volume Learning Explain Discontinuities in Cortical Maps?

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It has recently been shown that orientation and retinotopic position, both of which are mapped in primary visual cortex, can show correlated jumps (Das & Gilbert, 1997). This is not consistent with maps generated by Kohonen's algorithm (Kohonen, 1982), where changes in mapped variables tend to be anticorrelated. We show that it is possible to obtain correlated jumps by introducing a Hebbian component (Hebb, 1949) into Kohonen's algorithm. This corresponds to a volume learning mechanism where synaptic facilitation depends not only on the spread of a signal from a maximally active neuron but also requires postsynaptic activity at a synapse. The maps generated by this algorithm show discontinuities across which both orientation and retinotopic position change rapidly, but these regions, which include the orientation singularities, are also aligned with the edges of ocular dominance columns, and this is not a realistic feature of cortical maps. We conclude that cortical maps are better modeled by standard, non-Hebbian volume learning, perhaps coupled with some other mechanism (e.g., that of Ernst, Pawelzik, Tsodyks, & Sejnowski, 1999) to produce receptive field shifts.

1 Introduction ---

Kohonen's self-organizing feature mapping algorithm (Kohonen, 1982) and the elastic net algorithm (Durbin & Willshaw, 1987) have been remarkably successful in reproducing basic features of visual cortical maps (Durbin & Mitchison, 1990; Obermayer, Ritter, & Schulten, 1990; Obermayer, Blasdel, & Schulten, 1991; Swindale & Bauer, 1998). Durbin and Mitchison (1990) suggested that a type of complementarity principle should apply to these algorithms, according to which the spatial rates of change across the cortex of parameter values, such as preferred orientation or receptive field position, should be negatively correlated. Recently, however, Das and Gilbert (1997) reported in cat visual cortex the presence of fractures across which there were simultaneous jumps in preferred orientation and retinal receptive

field position. This appears to contradict the predictions of these otherwise highly successful algorithms. We examine here a modification of Kohonen's algorithm that can generate positively correlated large steps.

2 Kohonen's Algorithm and a Hebbian Variant

Kohonen's algorithm can be written as follows. Let \mathbf{r} denote a point in the two-dimensional cortical sheet, and let $\mathbf{f}(\mathbf{r})$ be the corresponding point in a parameter space representing stimulus values such as retinotopic position, ocular dominance, and orientation. Given a stimulus point \mathbf{S} in parameter space and some initial map that may be disordered or only partly ordered, one first determines the cortical point \mathbf{r}_m that maps closest to the stimulus, i.e. such that the distance $|\mathbf{f}(\mathbf{r}_m) - \mathbf{S}|$ is minimal. This can be interpreted as the cortical neuron that responds most strongly to the stimulus. The map \mathbf{f} is then updated by

$$\Delta \mathbf{f}(\mathbf{r}) = \varepsilon(S - f(r)) \exp \left\{ -|\mathbf{r} - \mathbf{r}_m|^2 / 2\sigma^2 \right\}, \quad (2.1)$$

where ε is a rate constant, and σ defines the width of the cortical neighborhood function that determines the extent to which neighboring points on the cortex move toward the stimulus \mathbf{S} . This process is repeated for many stimuli chosen at random from a functionally relevant set. This algorithm has a biological interpretation (Kohonen, 1993) in which the maximally responding cortical point \mathbf{r}_m is selected by an interaction involving lateral inhibition, and the movement of $\mathbf{f}(\mathbf{r})$ toward the stimulus \mathbf{S} represents the strengthening of synapses in the vicinity of \mathbf{r}_m whose inputs are activated by \mathbf{S} .

This rule is not strictly Hebbian. Instead equation 2.1 implies that active synapses within a certain distance of the neuron at \mathbf{r}_m are strengthened irrespective of the activity of the neuron they contact. This is consistent with experimental evidence for local spread of synaptic potentiation, which is independent of postsynaptic responses (Bonhoeffer, Staiger, & Aertsen, 1989; Schuman & Madison, 1994). Synaptic weight change based on this kind of local spread has been called "volume learning" (Gally, Montague, Reeke, & Edelman, 1990; Montague, Gally, & Edelman, 1991; Montague & Sejnowski, 1994). To obtain a more strictly Hebbian rule, we can require that change in $\mathbf{f}(\mathbf{r})$ occurs only if the neuron at \mathbf{r} is sufficiently active. In the parameter space formalism, this means that change occurs only if $|\mathbf{f}(\mathbf{r}) - \mathbf{S}|^2$ is sufficiently small. We can modify equation 2.1 to include this condition by setting

$$\Delta \mathbf{f}(\mathbf{r}) = \varepsilon(S - f(r)) \exp \left\{ -|\mathbf{f}(\mathbf{r}) - \mathbf{S}|^2 / 2\tau^2 \right\} \exp \left\{ -|\mathbf{r} - \mathbf{r}_m|^2 / 2\sigma^2 \right\}. \quad (2.2)$$

Here τ defines the width of a response function in parameter space. Equation 2.2 represents a kind of Hebbian volume learning. Such a rule was

proposed in another context, the optimization of cortical wiring, by Mitchison (1995).

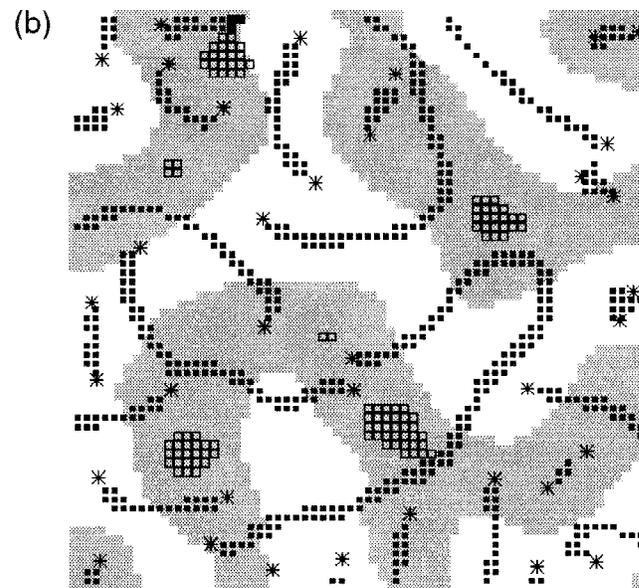
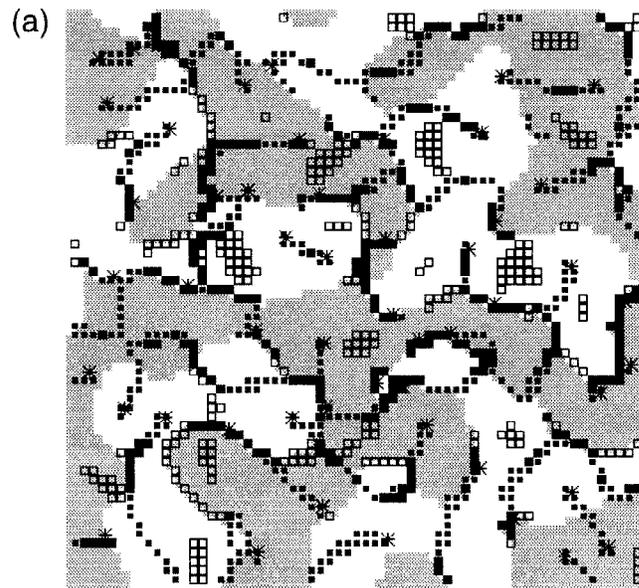
It is intuitively plausible that this modified algorithm can give rise to discontinuities in several variables at once. Suppose the map makes a large step in one variable. If the neurons on one side of the step map under f close to a stimulus \mathbf{S} , $|f(\mathbf{r}) - \mathbf{S}|$ will be large for neurons on the other side of the step and the first exponential in equation 2.2—the response of the neuron at \mathbf{r} to \mathbf{S} —will be small. Adjustment toward \mathbf{S} will therefore occur on only one side of the step, and the discontinuity will remain stable. Note that if the discontinuity was initially in only one variable, the fact that the development of receptive fields is decoupled across the step allows the other variables to evolve independently on either side of the step. Under the standard Kohonen rule, this effect is absent, and discontinuities tend to become smaller over time because points close in the cortex are drawn together when they are pulled toward a common stimulus point.

3 Simulated Maps and Correlated Steps

We generated maps using a parameter space with two dimensions of retinotopic position, one of ocular dominance, two of orientation, and two of direction selectivity (see Figure 1). To assess the behavior of discontinuities, we counted the number of cortical points where the gradient value for a particular variable exceeded a given threshold. We also counted the number of points where superthreshold steps occurred simultaneously in two variables, and we used this to compute a correlation index.

A measure of discontinuity was defined as follows: Given a cortical point (i, j) , the expression $\Delta = \sqrt{\{f(i, j) - f(i + 1, j)\}^2 + \{f(i, j) - f(i, j + 1)\}^2}$ was used to measure the change in orientation or direction selectivity between neighboring cortical points, f being the relevant angle. For retinotopic position, the changes in the two coordinates, f_1 and f_2 , were summed, giving $\Delta = \sum_{k=1,2} \sqrt{\{f_k(i, j) - f_k(i + 1, j)\}^2 + \{f_k(i, j) - f_k(i, j + 1)\}^2}$. Points were treated as discontinuities in a variable if Δ exceeded twice the value expected from a linear mapping. For example, if the mean spacing of iso-orientation domains on the cortex is λ lattice steps, then a linear map would change by $2\pi/\lambda$ radians per lattice step on the cortex. If Δ exceeds $4\pi/\lambda$, an orientation discontinuity is recorded. Direction and ocular dominance were handled analogously.

The top tables show the ratios n_i/N , n_i being the number of occurrences of discontinuity in the i th variable and N the total number of lattice points in the cortex. The ratio n_i/N can be regarded as an estimate of the probability $P(i) = P(\text{discontinuity in } i)$. The number of occurrences of discontinuities simultaneously in variables i and j is denoted by n_{ij} . The ratio n_{ij}/N is an estimate for the joint probability $P(i\&j) = P(\text{discontinuity in } i\&j)$. The lower tables show what we have called the correlation index, intended to measure



- * orientation singularity
- direction fracture
- retinal fracture
- retinal plus direction fracture

the extent to which the joint probability $P(i\&j)$ exceeds or falls below the expectation $P(i)P(j)$ for independence. We define

$$\text{Correlation index} = \{P(i\&j) - P(i)P(j)\} / \{P(i\&j) + P(i)P(j)\},$$

the denominator serving to keep the index within the bounds $-1 < \text{index} < 1$, the lower limit occurring for $P(i\&j) = 0$, and the upper limit for complete correlation, where $P(i\&j) = P(i) = P(j)$ and $P(i)$ is small.

Table 1 shows that this index is weak or negative in the standard Kohonen algorithm, but is strongly positive for all variable pairs in the Hebbian version. This latter behavior is similar in some respects to that reported by Das and Gilbert (1997). Visual inspection of the maps (see Figure 1a) shows that regions of rapid change in retinotopy are superposed to a large extent on regions where orientation and/or direction preference changes rapidly; this behavior does not occur with standard Kohonen maps (see Figure 1b).

However, other features of the Hebbian maps do not match the data well. Das and Gilbert (1997) found a strong correlation, $R = 0.81$ (given in their Table 1 as $R\text{-squared} = 0.66$), between gradient of orientation and gradient of receptive field position, both variables unthresholded. We find

Figure 1: *Facing page*. Representative maps obtained using the modified Kohonen algorithm (a) and the unmodified algorithm (b) showing relations between regions of relative discontinuity in different map parameters. Gray regions have ocular dominance values < 0 , and orientation singularities are indicated by asterisks. Square symbols show points for which the gradient exceeds the threshold defined in the legend to Table 1: small black squares represent regions of high direction gradient; unfilled squares are regions of high retinotopic gradient, and the larger black squares are regions where both retinal and direction gradients exceed threshold (for clarity, the corresponding regions for orientation are not shown). Note that in (a) the fracture regions, including the singularities and the edges of the ocular dominance columns, tend to coincide, whereas in (b) these regions tend to avoid each other.

Maps, from equation 1.1 or 1.2, were generated with a fixed cortical neighborhood function with $\sigma = 2.5$ grid points (corresponding approximately to $125 \mu\text{m}$ in our model cortex) and a cortex of 128×128 grid points. Orientation and direction coordinates of the stimuli lay on circles of radius = 1 with orientations randomly distributed and direction orthogonal to orientation, as described in Swindale and Bauer (1998); ocular dominance values were randomly $+1$ or -1 , and retinotopic coordinates uniformly distributed in the interval $[0, 16]$. Cortical values of orientation, direction, and ocular dominance were initially gaussian with mean values = 0 ± 0.1 ; the retinotopic map was initially ordered with a small random gaussian scatter of ± 0.5 retinal units. The "Hebbian" maps, from equation 1.2, assumed a fixed receptive field size, $\tau = 1$. These values correspond to plausible physiological values of orientation and direction tuning, and retinal receptive field size.

Table 1: Discontinuities in the Map Generated by the Unmodified Kohonen Algorithm and Its Hebbian Modification.

Discontinuity probabilities, Kohonen map				
Orientation				0.103
Direction				0.133
Ocular dominance				0.174
Retinotopy				0.026
Discontinuity probabilities, Hebbian Kohonen map				
Orientation				0.175
Direction				0.173
Ocular dominance				0.173
Retinotopy				0.153

	Orientation	Direction	Ocular Dominance	Retinotopy
Correlation index: Kohonen map				
Orientation	0.814			
Direction	-0.069	0.765		
Ocular dominance	-0.369	-0.007	0.703	
Retinotopy	-1	-0.644	-0.336	0.950
Correlation index: Hebbian Kohonen map				
Orientation	0.703			
Direction	0.532	0.705		
Ocular dominance	0.445	0.414	0.706	
Retinotopy	0.398	0.467	0.497	0.734

that this unthresholded correlation coefficient is negative for standard Kohonen maps ($R = -0.13$) and positive for the Hebbian maps ($R = 0.36$), but the correlation is far weaker for the Hebbian maps than for the data. Another unrealistic feature of the maps is that discontinuities in position and orientation coincide with abrupt changes in ocular dominance, the correlation thus extending to three variables simultaneously. This means that lines of orientation discontinuity, and thus the singularities, tend to coincide with the edges of ocular dominance stripes (see Figure 1a). Experimental data show that the singularities are found mostly in the centers of ocular dominance stripes (Bartfeld & Grinvald, 1992; Blasdel, 1992; Hübener, Shoham, Grinvald, & Bonhoeffer, 1997) and only occasionally on the edges (Bartfeld & Grinvald, 1992).

4 Conclusion

It does not seem plausible to “rescue” this application of Kohonen’s algorithm by including a term for postsynaptic activity. A useful inference can

be drawn from this conclusion. Since the attraction of fractures to the edges of ocular dominance columns seems to be a sensitive index of a Hebbian term, the absence of such a feature in real maps argues against a Hebbian component to the synaptic learning rule for maps. Thus, the models support standard volume learning rather than its Hebbian modification.

To explain Das and Gilbert's observations, some other mechanism must be invoked. Before embarking on too thorough an overhaul of models, however, it would be wise to wait until other species besides the cat have been examined. For instance, discontinuities are not seen in the retinotopic map in the tree shrew (Bosking, Crowley, & Fitzpatrick, 1997). If discontinuities do prove to be an important feature of cortical maps, one attractive way to model them would be to add the type of lateral interaction proposed by Ernst et al. (1999) to the standard Kohonen algorithm. It seems likely that a compound model of this sort would retain the successful features of Kohonen maps as well as introducing limited types of discontinuity.

References

- Bartfeld, E., & Grinvald, A. (1992). Relationships between orientation preference pinwheels, cytochrome oxidase blobs and ocular dominance columns in primate striate cortex. *Proc. Natl. Acad. Sci. USA*, *89*, 11905–11909.
- Blasdel, G. (1992). Orientation selectivity, preference, and continuity in monkey striate cortex. *J. Neurosci.*, *12*, 3139–3161.
- Bonhoeffer, T., Staiger, V., & Aertsen, A. (1989). Synaptic plasticity in rat hippocampal slice cultures: Local "Hebbian" conjunction of pre- and postsynaptic stimulation leads to distributed synaptic enhancement. *Proc. Natl. Acad. Sci. USA*, *86*, 8113–8117.
- Bosking, W. H., Crowley, J. C., & Fitzpatrick, D. (1997). Fine structure of the map of visual space in the tree shrew striate cortex revealed by optical imaging. *Soc. Neurosci. Abstr.*, *23*, 1945.
- Das, A., & Gilbert, C. D. (1997). Distortions of visuotopic map match orientation singularities in primary visual cortex. *Nature*, *387*, 594–598.
- Durbin, R., & Mitchison, G. (1990). A dimension reduction framework for understanding cortical maps. *Nature*, *343*, 644–647.
- Durbin, R., & Willshaw, D. J. (1987). An analogue approach to the traveling salesman problem using an elastic net method. *Nature*, *326*, 698–691.
- Ernst, U., Pawelzik, K., Tsodyks, M., & Sejnowski, T. (1999). Relation between retinotopical and orientation maps in visual cortex. *Neural Computation*, *11*, 375–379.
- Gally, J. A., Montague, P. R., Reeke, G. N., & Edelman, G. M. (1990) The NO hypothesis: Possible effects of a rapidly diffusible substance in neural development and function. *Proc. Natl. Acad. Sci. USA*, *87*, 3547–3551.
- Hebb, D. O. (1949). *The organization of behavior. A neuropsychological theory*. New York: Wiley.
- Hübener, M., Shoham, D., Grinvald, A., & Bonhoeffer, T. (1997). Spatial relationships among three columnar systems in cat area 17. *J. Neurosci.*, *17*, 9270–9284.

- Kohonen, T. (1982). Self-organized formation of topologically correct feature maps. *Biol. Cybern.*, *43*, 59–69.
- Kohonen, T. (1993). Physiological interpretation of the self-organizing map algorithm. *Neural Networks*, *6*, 895–905.
- Mitchison, G. (1995). A type of duality between self-organizing maps and minimal wiring. *Neural Computation*, *7*, 25–35.
- Montague, P. R., Gally, J. A., & Edelman, G. M. (1991). Spatial signalling in the development and function of neural connections. *Cerebral Cortex*, *1*, 199–220.
- Montague, P. R., & Sejnowski, T. J. (1994). The predictive brain: Temporal coincidence and temporal order in synaptic learning mechanisms. *Learning and Memory*, *1*, 1–33.
- Obermayer, K., Blasdel, G. G., & Schulten, K. (1991). A neural network model for the formation and for the spatial structure of retinotopic maps, orientation- and ocular-dominance maps. In T. Kohonen, K. Mäkisara, O. Simular, & J. Kangas (Eds.), *Artificial neural networks* (pp. 505–511). Amsterdam: Elsevier.
- Obermayer, K., Ritter, H., & Schulten, K. (1990). A principle for the formation of the spatial structure of cortical feature maps. *Proc. Natl. Acad. Sci. USA*, *87*, 8345–8349.
- Schuman, E. M., & Madison, D. V. (1994). Locally distributed synaptic potentiation in the hippocampus. *Science*, *263*, 532–536.
- Swindale, N. V., & Bauer, H.-U. (1998). Application of Kohonen's self-organizing feature map algorithm to cortical maps of orientation and direction preference. *Proc. R. Soc. Lond. B*, *265*, 827–838.

Received July 22, 1998; accepted October 29, 1998.