

01 **Chapter 45**  
02 **Cortical Anatomy and the Spatiotemporal**  
03 **Learning Rule**  
04  
05  
06

07 **J.J. Wright and P.D. Bourke**  
08  
09  
10  
11  
12

13 **Abstract** A model of the self-organization of synapses in the visual cortex is pre-  
14 sented. Subject to Hebbian learning with decay, evolution of synaptic strengths  
15 proceeds to a stable state in which all synapses have either maximum, or mini-  
16 mum, pre/post-synaptic coincidence. The most stable configuration gives rise to  
17 anatomically realistic “local maps”, each of macro-columnar size, and each or-  
18 ganized as Mobius projections of retinotopic space. A tiling of V1, constructed  
19 of approximately mirror-image reflections of each local map by its neighbors is  
20 formed, accounting for orientation-preference singularities, linear zones, and saddle  
21 points—with each map linked by connections between sites of common orientation  
22 preference. Ocular dominance columns, the occurrence of direction preference frac-  
23 tures always in odd numbers around singularities, and effects of stimulus orientation  
24 relative to velocity of motion, are accounted for. Convergence to this configuration  
25 is facilitated by the spatio-temporal learning rule.

26  
27 **Keywords**  
28  
29

AQ1

30 **Introduction**  
31

32 We have presented a theoretical account of the self-organization of synapses during  
33 development of the visual cortex (V1) [1]. This theory deduced the most stable con-  
34 figuration of synapses to emerge under a Hebbian learning rule. No consideration  
35 was given to pre-synaptic interaction, nor was a specific physiology of synaptic  
36 modification invoked. The spatiotemporal learning rule [2, 3] – which was devel-  
37 oped in relation to work in the hippocampus – allows for pre-synaptic interactions,  
38 and relates pre- and post-synaptic interactions to long-term-potential (LTP) and  
39 depression (LTD). This paper summarizes the earlier theory of V1 self-organization,  
40 and concludes with comments on the relevance of the spatiotemporal rule in this  
41 further anatomical context.

42  
43 

---

44 J.J. Wright  
45 Department of Psychological Medicine, University of Auckland, Auckland, New Zealand  
e-mail: jj.w@xtra.co.nz

## Theory

### *Synaptic Densities in V1*

In V1 and cortex generally, the density of synaptic couplings generated by each neuron declines with distance from the soma of the cell of origin, at two principal scales – that of the local intra-cortical connections (at the V1 macrocolumnar scale), versus the longer intracortical connections spanning a substantial fraction of the extent of the V1, which are continuous with interareal connections [4, 5, 6]. Via polysynaptic transmission, information can reach each macrocolumn-sized area, from the whole, or a substantial part, of V1, thus modulating direct visual pathway inputs. We will describe the emergent unit organization on the smaller, macrocolumnar, scale as the *local map*, and V1 itself as the *global map*.

### *Visual Cross-Correlation and Synchronous Fields*

Because of the decline of synaptic density with distance, the spatial covariance of activity (synchronous oscillation) between any pair of pyramidal neurons in V1 declines with distance [7, 8, 9, 10]. Visual stimuli exhibit a decline in spatial covariance with distance, and impose this property upon activity in V1. Thus, covariance of activity in V1 declines with distance at both the global, V1, scale, and the local, macro-columnar, scale, and as will be shown, this provides a metric for organization of connections.

### *Learning Rule*

A simple Hebbian rule, with decay can be initially applied. At each synapse the co-incidence of pre and post synaptic activity,  $r_{Q\varphi}$ , over a short epoch,  $t$ , is given by

$$r_{Q\varphi}(t) \propto \sum_t Q_e(t) \times \varphi_e(t) \quad (45.1)$$

where  $Q_e(t) \in \{0, 1\}$  is the post-synaptic firing rate, and  $\varphi_e(t) \in \{0, 1\}$  is the pre-synaptic firing rate. A Hebbian multiplication factor,  $H_s$ , operating on the gain of synapses at steady states of pre- and post-synaptic firing is given as

$$H_s = H_{\max} \exp[-\lambda/r_{Q\varphi}] \quad (45.2)$$

where  $\lambda$  is a suitable constant. With changes in  $r_{Q\varphi}$ ,  $H_s$  can increase or decline over time.

### Stability at Individual Synapses

It is shown in [1] that under this learning rule synapses can approach a stable state, only by approaching either one of two extremes – either *saturated* or *sensitive*.

In the saturated state,  $H_s$  and  $r_{Q\phi}$  are at maxima, while in the sensitive state,  $H_s$  and  $r_{Q\phi}$  are at minima. Conversely,  $\frac{dH_s}{dr_{Q\phi}}$ , the sensitivity to change in synaptic gain, is at a minimum for saturated synapses and a maximum for sensitive synapses – hence the choice of the names. No specific physiological state was assumed as the basis of saturation or sensitivity.

### Metabolic Uniformity

Competition occurring for metabolic resources within axons adds a constraint to Hebbian rules [11]. Metabolic energy supply of all small axonal segments remains approximately uniform, while the metabolic demand of saturated synapses, which have high activity, will be much greater than for sensitive synapses. Therefore the proportion of saturated and sensitive synapses must be approximately uniform along axons, and consequently the densities of both saturated and sensitive synapses must decline with distance of pre-synapses from the cell bodies of origin.

### The Impact of Distance/Density and Saturation/Sensitivity on Overall Synaptic Stability

All positions in V1,  $\{P_{j,k}\}$ , can be given an ordered numbering in the complex plane,  $1 \dots, j, \dots, k, \dots, 2n$ , and all positions within a macrocolumn located at  $P_0$ ,  $\{P_{j,k}\}$ , can be similarly numbered. The total perturbation of synaptic gains for the synapses from V1 entering the macrocolumn,  $\Psi(pP)$ , and the total perturbation of synaptic gains within the macrocolumn,  $\Psi(pp)$ , can thus be written as

$$\Psi(pP) = \sum_{j=1}^{j=n} \sum_{k=1}^{k=n} \sigma_{SAT}(p_j P_k) S_{SAT}(p_j P_k) + \sum_{j=1}^{j=n} \sum_{k=1}^{k=n} \sigma_{SENS}(p_j P_k) S_{SENS}(p_j P_k) \quad (45.3)$$

$$\Psi(pp) = \sum_{j=1}^{j=n} \sum_{k=1}^{k=n} \sigma_{SAT}(p_j p_k) S_{SAT}(p_j p_k) + \sum_{j=1}^{j=n} \sum_{k=1}^{k=n} \sigma_{SENS}(p_j p_k) S_{SENS}(p_j p_k) \quad (45.4)$$

where  $\sigma_{SAT}(p_j P_k, p_j p_k)$  and  $\sigma_{SENS}(p_j P_k, p_j p_k)$  are densities of saturated and sensitive synapses respectively, and  $S_{SAT}(p_j P_k, p_j p_k)$  and  $S_{SENS}(p_j P_k, p_j p_k)$  are the corresponding variations of synaptic gains over a convenient short epoch.

01 Since densities of synapses decline with distances of cell separation, then as a  
 02 simple arithmetic property of sums of products, minimization of  $\Psi(pp)$  requires  
 03 neurons separated by short distances to most closely approach maximum saturation,  
 04 or maximum sensitivity. Yet metabolic uniformity requires that both sensitive  
 05 and saturated synaptic densities must decline with distance from the cell bodies  
 06 of origin, and remain in equal ratio. An apparent paradox arises, since sensitive  
 07 synapses must link pre- and post-synaptic neurons with minimal pre- and post-  
 08 synaptic pulse co-incidence, yet the reverse is true for saturated synapses. Also ap-  
 09 parently paradoxically, minimization of  $\Psi(pP)$  requires that saturated connections  
 10 afferent to any  $p_j$  arise from highly covariant, and therefore closely situated, sites  
 11 in V1, while sensitive connections afferent to  $p_j$  must arise from well-separated  
 12 sites. Yet again, metabolic uniformity requires that both sensitive and saturated  
 13 pre-synapses arise from cells at any single site. The paradoxes exist only in the  
 14 Euclidean plane, and can be resolved as follows.

15

16

### 17 ***Mobius Projection, and the Local Map***

18

19 By re-numbering  $\{P_{j,k}\}$  as  $\{P_{j1,j2,k1,k2}\}$ , and  $\{p_{j,k}\}$  as  $\{p_{j1,j2,k1,k2}\}$ , the subscript  
 20 numbers  $1, \dots, j1, \dots, j2, \dots, n, (n+1), \dots, j2, \dots, k2, \dots, 2n$  can be ascribed  
 21 in the global map so that  $j1$  and  $j2$  are located diametrically opposite and equidis-  
 22 tant from  $P_0$ , while in the local map  $j1$  and  $j2$  have positions analogous to superim-  
 23 posed points located on opposite surfaces of a Mobius strip. This generates a *Mobius*  
 24 *projection* (the *input map*) from global to local, and a *Mobius ordering* within the  
 25 local map. That is,

26

$$27 \frac{P_{jm}^2}{|P_{jm}|} \rightarrow p_{km} \quad m \in \{1, 2\} \quad (45.5)$$

28

$$29 p_{jm} \rightarrow p_{km} \quad m \in \{1, 2\} \quad (45.6)$$

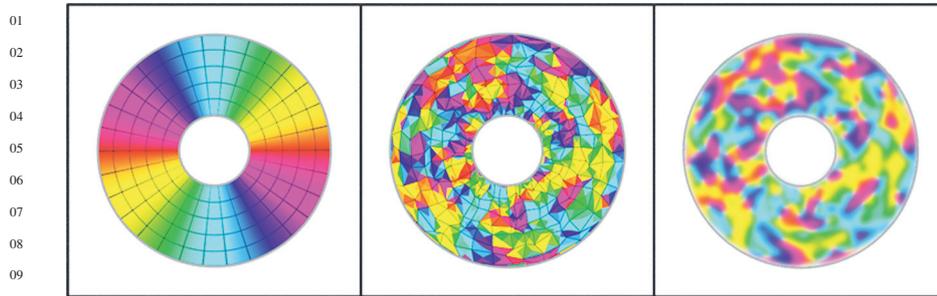
30

31 In Eq. (45.5) the mapping of widely separated points in the global map converge  
 32 to coincident points on opposite surfaces of the local map's Mobius representation.  
 33 In the Eq. (45.6) the density of saturated synaptic connections now decreases as  
 34  $|j1-k1|$  and  $|j2-k2|$ , while the density of sensitive couplings decreases as  $|j2-k1|$   
 35 and  $|j1-k2|$ .

36

37 The anatomical parallel requires  $j1$  and  $j2$  in the local map to represent two  
 38 distinct groups of neurons. To attain maximum synaptic stability within the local  
 39 map an intertwined mesh of saturated couplings forms, closed after passing twice  
 40 around the local map's centre, with sensitive synapses locally linking the two turns  
 41 of the mesh together. In this fashion both saturated and sensitive synapses decline  
 42 in density with distance, as required. The input map is of corresponding form, con-  
 43 veying an image of the activity in V1 analogous to projection onto a Mobius strip.

44 Evolution of these patterns of synaptic connections is shown in Figs. 45.1  
 45 and 45.2.



10  
11 **Fig. 45.1** Initial conditions for local evolution of synaptic strength. *Left:* The global field (V1) in polar co-ordinates. Central defect indicates the position of a local area of macro-columnar size. Polar angle is shown by the color spectrum, twice repeated. *Middle:* Zones of random termination (shown by color) of lateral axonal projections from global V1 in the local area. Central defect is an arbitrary zero reference. *Right:* Transient patterns of synchronous oscillation generated in the local area, mediated by local axonal connections

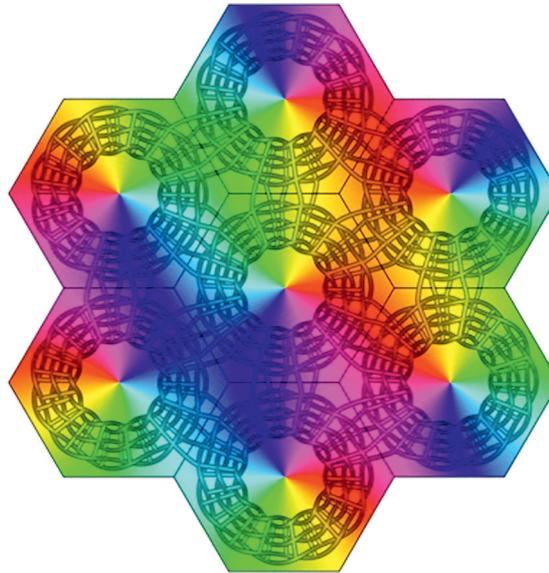


28 **Fig. 45.2** Evolution of synaptic strengths to their maximally stable configuration. *Left:* The global field (V1), as represented in Fig. 45.1. *Middle:* Saturated synaptic connections input from the global field now form a Möbius projection of the global field, afferent to the local map, forming an input map. *Right:* Saturated local synapses within the local map form a mesh of connections closed over  $0-4\pi$  radians. The central defect now corresponds to the position within the local map, of the local map within the global map. Sensitive synapses (not shown) link adjacent neurons as bridges between the  $0-2\pi$  and  $2\pi-4\pi$  limbs of the mesh of saturated connections. Wright et al. 2006

### 36 *Monosynaptic Interactions Between Adjacent Local Maps*

37  
38  
39 The input and local maps can, in principle, emerge with any orientation, and with  
40 either left or right-handed chirality. However, chirality and orientation of adjacent  
41 local maps is also constrained by requirement for overall stability. Adjacent local  
42 maps should form in approximately mirror image relation, as shown in Fig. 45.3,  
43 because in that configuration homologous points within the local maps have densest  
44 saturated and sensitive synaptic connections, thus meeting minimization require-  
45 ments analogous to those of Eq. 45.3a,b.

01 **Fig. 45.3** Organization of  
 02 saturated coupling within and  
 03 between local maps, and the  
 04 approximate mirror  
 05 symmetry of orientation  
 06 preference in adjacent local  
 07 maps [1]



08  
09  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20 ***Consequences of Projection of Object Configuration***  
 21 ***and Motion from the Global to the Local Map***  
 22

23 The emergent input and local maps form a 1:1 representation of points in the global  
 24 map. As described in [1], this accounts for response preferences of V1 neurons to  
 25 visual stimuli – notably orientation preference singularities, linear zones and saddle  
 26 points, and connections between cells of similar orientation preference in adjacent  
 27 macrocolumns [12]. Ocular dominance columns [13], which arise in parts of V1  
 28 with binocular input, can be explained as a special case of the application of similar  
 29 mechanisms to those operating in monocular cortex. The occurrence of direction  
 30 preference fractures always in odd numbers around singularities [14] is explained  
 31 by the Möbius configuration of the local map, and axonal conduction lags from the  
 32 global to the local maps accounts for the dynamic variation of orientation preference  
 33 which occurs with changes in stimulus velocity when, stimulus orientation is not  
 34 orthogonal to the direction of motion [15].  
 35  
 36

37 ***Application of the Spatiotemporal learning Rule***  
 38 ***and its Relationship to LTP and LTD***  
 39  
 40

41 The explanation of self-organization of the synaptic connections in V1 given in [1]  
 42 is deficient in two respects.

43 Firstly, no particular physiological synaptic mechanism is associated with the de-  
 44 scriptive terms “saturated” and “sensitive”, and these idealized states may never be  
 45 attained physiologically. However, at least on the appropriate time-scale, saturation

01 of a synapse may be equated with the LTP state, and sensitivity of a synapse with  
02 the LTD state, as indicated in [2, 3].

03 Secondly, the approach of all synapses to their maximally stable condition has  
04 been assumed, without any mechanism being proposed to assist convergence to-  
05 wards maximum stability. The spatiotemporal rule has been recently specified in  
06 relation to LTD/LTP of conventional Hebbian type [16]. The operation of this learn-  
07 ing rule, which facilitates the mapping of adjacent afferent connections, has the  
08 properties required to bring about convergence to stability, since the global-to-local  
09 mapping depends on the preservation of the same relation between spatial covari-  
10 ance and distance at both local and global levels.

## 12 References

- 14 1. Wright JJ, Alexander DM, Bourke PD (2006) Contribution of lateral interactions in V1 to  
15 organization of response properties. *Vision Research* 46: 2703–2720.
- 16 2. Tsukada M, Aihara T, Saito H (1996) Hippocampal LTP depends on spatial and temporal  
17 correlation of inputs. *Neural Networks* 9: 1357–1365.
- 18 3. Tsukada M, Pan X (2005) The spatio-temporal learning rule and its efficiency in separating  
19 spatiotemporal patterns. *Biological Cybernetics* 92: 139–146.
- 20 4. Scholl DA (1956) *The Organization of the Cerebral Cortex*. Wiley, New York.
- 21 5. Braitenberg V, Schuz A (1991) *Anatomy of the Cortex: Statistics and Geometry*. Springer-  
22 Verlag, New York.
- 23 6. Liley DTJ, Wright JJ (1994) Intracortical connectivity of pyramidal and stellate cells: esti-  
24 mates of synaptic densities and coupling symmetry. *Network* 5: 175–189.
- 25 7. Wright JJ (1997) EEG simulation: variation of spectral envelope, pulse synchrony and 40 Hz  
26 oscillation. *Biological Cybernetics* 76: 181–184.
- 27 8. Robinson PA, Rennie CJ, Wright JJ (1998) Synchronous oscillations in the cerebral cortex.  
28 *Physical Review E* 57: 4578–4588.
- 29 9. Wright JJ, Bourke PD, Chapman CL (2000) Synchronous oscillation in the cerebral cortex and  
30 object coherence: simulation of basic electrophysiological findings. *Biological Cybernetics*  
31 83: 341–353.
- 32 10. Chapman CL, Bourke PD, Wright JJ (2002) Spatial eigenmodes and synchronous oscillation:  
33 coincidence detection in simulated cerebral cortex. *Journal of Mathematical Biology* 45: 57–78.
- 34 11. Grossberg S, Williamson JR (2001) A neural model of how horizontal and interlaminar con-  
35 nections of visual cortex develop into adult circuits that carry out perceptual grouping and  
36 learning. *Cerebral Cortex* 11: 37–58.
- 37 12. Bosking WH, Zhang Y, Schofield B, Fitzpatrick D (1997) Orientation selectivity and the ar-  
38 rangement of horizontal connections in tree shrew striate cortex. *Journal of Neuroscience* 17:  
39 2112–2127.
- 40 13. Obermayer K, Blasdel GG (1993) Geometry of orientation and ocular dominance columns in  
41 monkey striate cortex. *Journal of Neuroscience* 13: 4114–4129.
- 42 14. Swindale NV, Shoham D, Grinvald A, Bonhoeffer T, Hubener M. (2000) Visual cortical maps  
43 are optimised for uniform coverage. *Nature Neuroscience* 3: 822–826.
- 44 15. Basole A, White LE, Fitzpatrick D (2003) Mapping multiple features of the population re-  
45 sponse of visual cortex. *Nature* 423: 986–990.
16. Tsukada M, Yamazaki Y, Kojima H (2007) Interaction between the spatiotemporal learning  
rule (STRL) and Hebb type (HEBB) in single pyramidal cells in the hippocampal CA1 area.  
(in submission).

01  
02  
03  
04  
05  
06  
07  
08  
09  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45

UNCORRECTED PROOF