Springer-Verlag Berlin Heidelberg New York
London Paris Tokyo Hong Kong Barcelona
Budapest

Blobs or Slabs - is that the Question?

Siegrid Löwel

Max-Planck-Institut für Hirnforschung, Deutschordenstr. 46, 6000 Frankfurt a. M. 71, Germany

Theoretical models and hypotheses are the basis of any experimental work. Their predictive value has to be tested by appropriate experiments in order to select those concepts that are more viable than others.
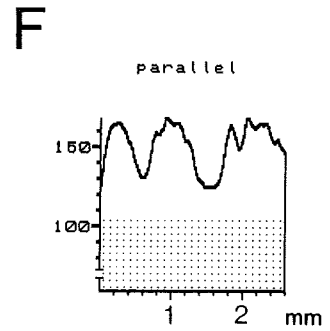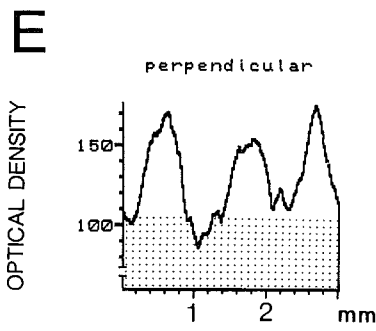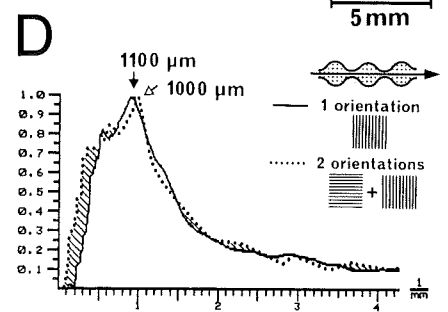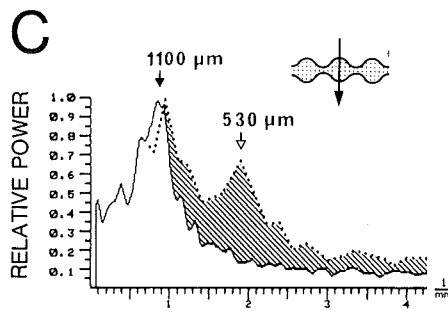
It is a well established phenomenon of cortical organization that neurones are not scattered randomly but clustered together according to specific response properties. In visual cortex, cells recorded along electrode penetrations perpendicular to the cortical layers were found to respond to similarly oriented lines whereas a gradual shift of orientation preference was observed along tangential penetrations (Hubel and Wiesel 1959, 1974; Albus 1975). The development of the 2-deoxy-glucose (2-DG) method by Sokoloff et al. (1977) allowed to map the topographical arrangement of iso-orientation columns more comprehensively than with electrophysiological techniques (i.e. Albus 1979; Singer 1981; Hubel et al. 1977; Humphrey et al. 1980). This approach revealed that iso-orientation domains frequently have the shape of slabs and bands rather than of isolated columns. Two mathematical models about the development of orientation selectivity (Swindale 1982; von der Malsburg and Cowan 1982) also inferred that iso-orientation domains should be arranged as *parallel* and regularly spaced slabs with trajectories essentially orthogonal to area boundaries. An alternative geometrical concept has been put forward by Braitenberg and Braitenberg (1979) in which orientations are proposed to be arranged *radially* around centers. A 2-DG study in our laboratory directly tested the validity of the two alternative concepts by comparing activity patterns in the cat visual cortex induced by visual stimulation with gratings of various orientations (Löwel et al. 1987).

If iso-orientation domains are arranged as parallel bands i) the trajectories of the 2-DG bands must be invariant to changes in stimulus

orientation and ii) presentation of horizontal and vertical contours should lead to similar patterns except that the spacing of activated bands should be reduced by a factor of 0.5 (doubling of the spatial frequency composition of the 2-DG patterns). If - on the other hand - Braitenbergs' concept is right i) the trajectories of activated iso-orientation domains should change with stimulus orientation and ii) stimulation with orthogonal contours should activate short slabs of cortical tissue that are orthogonal to each other (no change in the spatial frequency composition). Figure 1 summarizes the main results of this study. Visual stimulation with gratings of a single orientation induced highly ordered patterns of increased 2-DG uptake consisting of regularly spaced and beaded stripes (B) with a mean distance of 1.0 - 1.2 mm (C). Stimulation with two orthogonal orientations led to patterns with similar general layout (A) but with "twice as many" stripes: one-dimensional Fourier analyses perpendicular to the main trajectories of the bands revealed an additional peak at the doubled spatial frequency (C). Similar analyses parallel to the iso-orientation bands revealed no major differences in the spectra between the single and double stimulated visual cortices (D). Additional two-dimensional Fourier analyses also confirmed that stimulation with two rather than with one orientation increased the spatial frequency content of the 2-DG patterns along vectors perpendicular to the bands but not along vectors parallel to the bands.

Finally I would like to present some data concerning the ongoing discussion whether iso-orientation domains consist of elongated slabs (which can be assigned a certain trajectory) or isolated columns. Optical density measurements along vectors perpendicular (E) resp. parallel

Fig. 1. A, B: After all these theories some "real" cortical maps: 2-DG autoradiographs of flat-mounts of the left (A) and right (B) visual cortices of a cat. The animal was stimulated in its right visual hemifield with horizontal and vertical gratings that were presented in alternation and in its left visual hemifield with a vertically oriented grating only. C, D: The spatial frequency composition of the autoradiographs as determined by one-dimensional Fourier analyses. Average of measurements along vectors perpendicular (C) resp. parallel (D) to the main trajectories of the iso-orientation bands in the single (solid line) and double (dotted line) stimulated hemispheres. Note that the second peak at doubled spatial frequency occurs only after stimulation with two orientations and only in measurements perpendicular to the iso-orientation bands (dotted line in C). E, F: Optical density measurements perpendicular (E) and parallel (F) to the bands. Note that the radioactive labeling along the bands is always higher than between them (dotted area). Abbreviations: a = anterior, p = posterior

A

B

5mm

C

RELATIVE POWER

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1

1100 µm

530 µm

1 mm

D

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1

1100 µm

1000 µm

1 orientation

2 orientations

1 mm

SPATIAL FREQUENCY

E

OPTICAL DENSITY

perpendicular

150

100

1   2   mm

F

parallel

150

100

1   2   mm

(F) to the "bands" demonstrate i) a periodic fluctuation in radioactive labeling in both cases (due to the bands (E) resp. beads (F)) and more importantly ii) that radioactive labeling along the "bands" is always higher than between them. Thus the autoradiographs exhibit a specific asymmetry in their optical density distribution which is more suggestive of a parallel than of a radial arrangement of activated regions.

Taken together these results are compatible with the hypothesis that stimulation with two orientations activates twice as many parallel orientation bands than stimulation with a single orientation. Thus, our data indicate that cortical regions containing neurones with similar orientation preference have the form of elongated slabs that run parallel to each other and that interdigitate with iso-orientation slabs encoding different orientations. Our results are definitively *not* compatible with Braitenbergs' hypothesis about the geometry of cortical line detectors because i) trajectories of iso-orientation domains do not change with stimulus orientation and ii) stimulation with orthogonal contours induces activity patterns with doubled spatial frequency content. Our results may however be compatible with a more recent variation of the radial arrangement theme proposed by Götz (1988). In this model, all orientations occur only once on a circular trajectory around the center. Indeed there are already some results from optical recording experiments in monkey V1 and cat area 18 which do support the Götz concept (Blasdel and Salama 1986; Bonhoeffer and Grinvald, this volume).

In the end, the reader may ask what do we learn at all from knowing the exact topography of the orientation domains. Is this all not just "l'art pour l'art" or some meaningless academical dispute? It is our belief that these maps or representations of particular functional properties are the result of an ontogenetic process and are "shaped" by experience. It is hoped that knowledge of their layout may help to elucidate the underlying developmental mechanisms and eventually contribute to the fundamental question why neurones with similar response characteristics are clustered at all.

References

Albus K (1975) A quantitative study of the projection area of the central and the paracentral visual field in area 17 of the cat. II. The spatial organization of the orientation domain. Exp Brain Res 24:181-202

Albus K (1979) ^{14}C-deoxyglucose mapping of orientation subunits in the cat's visual cortical areas. Exp Brain Res 37:609-613

Blasdel GG, Salama G (1986) Voltage-sensitive dyes reveal a modular organization in monkey striate cortex. Nature 321:579-585

Braitenberg V, Braitenberg C (1979) Geometry of orientation columns in the visual cortex. Biol Cybern 33:179-186

Götz KG (1988) Cortical templates for the self-organization of orientation-specific *d*- and *l*-hyper-columns in monkeys and cats. Biol Cybern 58:213-223

Hubel DH, Wiesel TN (1959) Receptive fields of single neurones in the cat's striate cortex. J Physiol (L) 148:574-591

Hubel DH, Wiesel TN (1974) Sequence regularity and geometry of orientation columns in the monkey striate cortex. J Comp Neurol 158:267-294

Hubel DH, Wiesel TN, Stryker MP (1977) Orientation columns in macaque monkey visual cortex demonstrated by the 2-deoxyglucose autoradiographic technique. Nature 269:328-330

Humphrey AL, Skeen LC, Norton TT (1980) Topographic organization of the orientation column system in the striate cortex of the tree shrew (Tupaia glis). II. Deoxyglucose mapping. J Comp Neurol 192:549-566

Löwel S, Freeman B, Singer W (1987) Topographic organization of the orientation column system in large flat-mounts of the cat visual cortex: a 2-deoxyglucose study. J Comp Neurol 255:401-415

Singer W (1981) Topographic organization of orienation columns in the cat visual cortex. Exp Brain Res 44:431-436

Sokoloff L, Reivich M, Kennedy C, Des Rosiers MH, Patlak CS, Pettigrew KD, Sakurada O, Shinohara M (1977) The (^{14}C)deoxyglucose method for the measurement of local cerebral glucose utilization: Theory, procedure, and normal values in the conscious and anesthetized albino rat. J Neurochem 28:897-916

Swindale NV (1982) A model for the formation of orientation columns. Proc R Soc Lond (B) 215:211-230

von der Malsburg C, Cowan JD (1982) Outline of a theory for the ontogenesis of iso-orientation domains in visual cortex. Biol Cybern 45:49-56