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"Neural Computation in the Visual Cortex"

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Neural Computation in the Visual Cortex

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1 Cortical Architecture and Spatio-temporal Receptive Field Organization

1.1 General Features of Cortical Cytoarchitectonics

- Cortical areas contain huge numbers of neurons ($> 10^{10}$) that are hard to model individually. In area 17, the cortical neurons outnumber the thalamic input fibers by a factor of 10^2 to 10^3.
- Cortex is a two-dimensional structure which is *uniform* in the horizontal direction (at least within an area). As to the vertical organization, it shows more or less pronounced *layering* (layers are numbered from I to VI).
- The most common type of neuron (approx. 70 % in mouse visual cortex) is the *pyramidal cell* which is characterized by vertically extending dendritic trees. These are often segmented into a roughly spherical 'basal dendrite' surrounding the soma and an 'apical dendrite' extending from the soma upwards (piad). Pyramidal cells have dendritic spines. They are considered excitatory.
- Some 20 % of cortical cells have roughly spherical dendritic and axonal arborizations. The *spiny stellate cells* resemble pyramidal cells while the *non-spiny stellate cells* are inhibitory.
- Pyramidal cells receive in the order of 10^4 synaptic inputs. In general, the density of synapses is about one per μm of dendritic fiber. Within the dendritic range of an average pyramidal cell, there are about 4000 other pyramidal cells.
- Pyramidal cell axons have collaterals branching in the vicinity and below the soma. These may be 'recurrent', i.e. running piad above the soma.

1.2 The Model

Stimulus, excitation, and coupling are described by continuous functions. The coupling strength of two neurones (i.e. two points in the continuous description) is given as the overlap of the corresponding dendritic and axonal 'clouds' (cf. Fig. 1).

Important features of the model are: Distributed positive feedback, average effects of large numbers of neurons, effects of propagation times are included. Nonlinear versions of the model are under investigation.

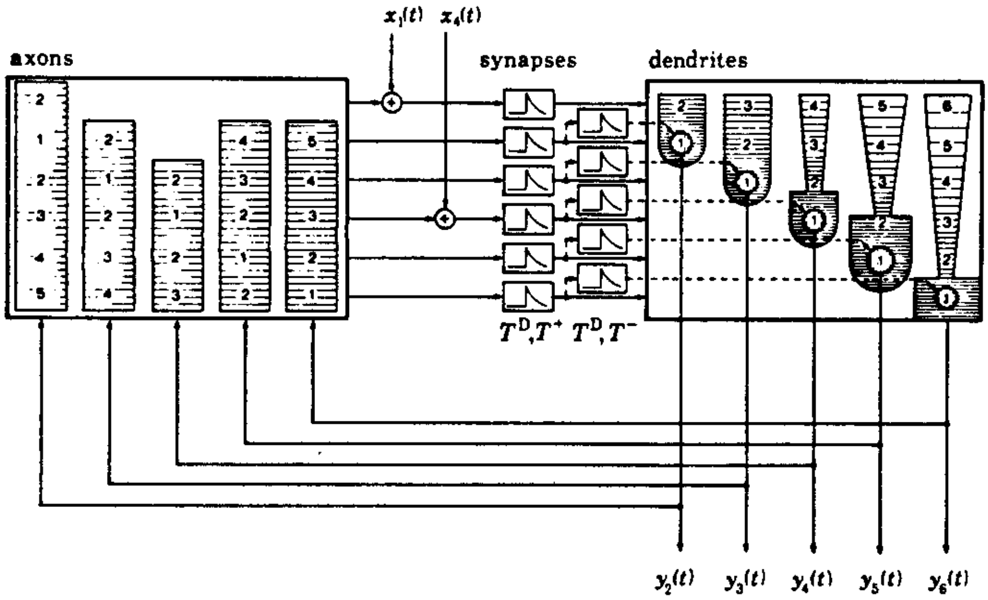

Figure 1: Computational structure of the model. Let a small region of layer IV be stimulated by an input $x_4(t)$. After a time delay T^D and low-pass filtering (time constant T^+) at the excitatory synapses, the cells sending dendrites to the stimulated region will be activated. In the next step the excitation $y_2, \ldots, y_6$ of the cells will spread over the axonal arborizations. The sum of activity in each layer together with the external input forms the instantaneous presynaptic activity. This presynaptic activity in each layer (I - VI) contributes to the excitation of all neurons sending dendrites to this layer. The dashed lines represent the inhibition which is transferred by an additional synapse and acts on the cells within the vertically hatched region.

1.3 Predictions

The model computes spatio-temporal responses to various stimuli. In the linear space-invariant case, these can be identified with receptive field profiles. Specific predictions include

- Excitation oscillates in a time range of about 5 Hz.
- Since the first peak of this oscillation can be rather small, large 'latencies' can occur.
- Spatio-temporal non-separability, i.e., the receptive field function $f(x, y, t)$ can not be written as a product of the form $g(x, y) \cdot h(t)$. As a consequence, the temporal structure of the stimulus influences the spatial operation applied to it.
- Tuning characteristics (e.g. hypercomplexity) should be time dependend.

1.4 Electrophysiology

Detailed recordings of spatio-temporal receptive field characteristics in the cat visual cortex (Best et al. 1988) show that most of these predictions hold.

- Latencies and oscillations

- Spatio-temporal non-separability can be directly observed in temporal sequences of 2D receptive field profiles.
- Types of non-separability: piecewise, looming-type, motion-type.
- Hypercomplexity changes with the speed of a moving bar.
- Orientation-tuning in on-off stimulation is different for different peaks in the PSTH.

1.5 Conclusion

Cortical image processing is spatio-temporal, i.e., it uses spatio-temporal features rather than static ones. Complicated non-separable interactions of spatial and temporal response behavior can be explained by distributed possitive feedback.

1.6 Reading List

Best, J., Mallot, H. A., Krüger, K., Dinse, H. R. O. 1988: Dznamics of visual information processing in cortical systems. In: Dreyfus, G. & Personnaz, L. (Eds.): *Proceedings nEuro-88.* In press.

Braitenberg, V. & Lauria, F. 1960: Towards a mathematical description of the grey substance of nervous systems. *Nuovo Cimento* Suppl. **18**, Serie 10, 1135-1151.

Krone, G., Mallot, H. A., Palm, G., Schüz, A. 1986: Spatiotemporal receptive fields: a dynamical model derived from cortical architectonics. Proc. Roy. Soc. Lond. B **226**, 421-444.

Sholl, D. A. 1955: The organization of the visual cortex in the cat. *J. Anat.* (London) **89**, 33-46.

Wilson, H. R. & Cowan, J. D. 1973: A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue. *Kybernetik (= Biol. Cybern.)* **13**, 55-80.

2 Retinotopic Mapping as a Tool for Information Processing

2.1 Cortical Representation of Sensory Surfaces

Visual, auditory, and somatosensory cortex areas are receptotopically organized. Different animals as well as different areas in multiple representations of the same modality often have different maps. Projections of one cortex area to another usually involve mappings as well, i.e., they preserve some spatial information. Different types of mappings (or, rather, ideas how to describe them) are:

Topographic Mapping One-to-one, piecewise continuous representation. The input to the target area is a distorted version of the excitation in the source area. Good examples are the maps of the visual space in areas 17, 18, 19.

Space-variant Filter Many-to-many. Connectivity is defined as a weight for each pair of points in source- and target area. The weights connected to a fixed point in the source area are called its *point-spread-function*; those connected to a point in the target area *receptive fields.* In general, space-variant filters need not be mappings at all. An additional requirement is that receptive fields are sufficiently small (or sharply tunes) and their position (or other properties) changes as the location in the target area changes.

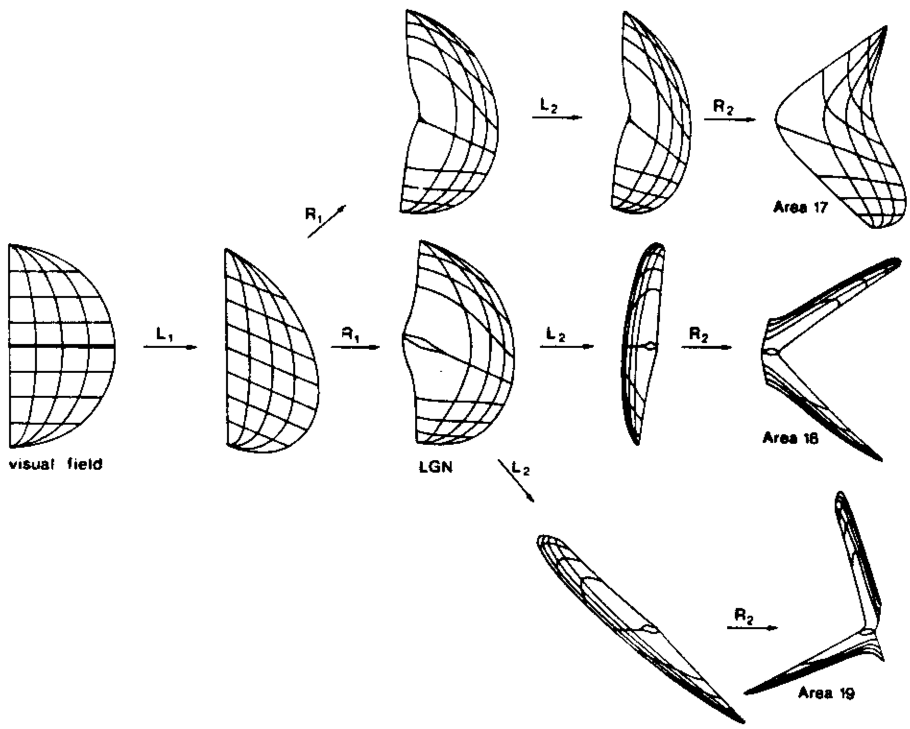

Figure 2: Construction of the topographic maps of areas 17, 18, and 19 in the cat's visual cortex as a composition of steps. The visual field is represented by a grid of spherical polar coordinates. The first two steps are basically the same for all three mappings and give a reasonable approximation of the LGN map. The steps $\mathcal{R}_1$ and $\mathcal{R}_2$ combine to the complex power function. $\mathcal{R}_2$ is responsible for the branching of the horizontal meridian in the maps of areas 18 and 19. Since this branching occurs in the left half of the complex power function (arguments with real part < 0), a mirroring is included in these two pathways ($\mathcal{L}_2$).

Patchy Connectivity This occurs if two or more source areas compete for representation in the same target area. Similar to topographic mapping. A well known example are the ocularity stripes in area 17, where input from different layers of the Lateral Geniculate Nucleus is combined. In general, patchy connectivity may or may not have overlap.

Columnar Organization This refers to a spatial variation of intrinsic organization (such as orientation selectivity). Actually, it is not a mapping at all. However, in effect, it leads to a spatial variation of receptive field properties as well.

Parametric Mapping This is just another way to look at an ordinary mapping: once it is established, local image processing operations perform complicated tasks when interpreted in terms of the original input. There are few convincing examples of this type.

2.2 Mapping Functions for Topographic Maps

Topographic mappings can be described by mathematical functions that assign a location $\mathbf{y}$ in the target area to every location $\mathbf{x}$ in the source area, i.e. $\mathbf{y} = \mathcal{R}(\mathbf{x})$. A number of constraints can be named for these functions that have to be observed in their construction:

- In accordance with the definition of a topographic mapping, we require that the mapping be one-to-one and piecewise continuous and smooth.
- Some authors have stressed the point that topographic mappings should be conformal. However, there are counterexamples, such as the representation of the lower visual field in the cat's area 17.
- Electrophysiological measurements provide data on *magnification factors*. Areal magnification corresponds to the absolut value of the Jacobian of the mapping function.
- Approximation of maps should use concatenations rather than sums of maps, since concatenations have natural interpretations as sequences of mappings in the visual pathway.

2.3 The Mappings of Area 17, 18, and 19 of the Cat

Magnification factors, branching of horizontal meridian, differences between the representations of upper and lower visual field, conformality. A model is presented in Fig. 2.

2.4 Functional Interpretations

Complex Logarithm: rotation- and scale-invariance for pattern recognition, scale-invariant filtering, optical flow.

Algebraic groups of mappings: more general invariances in pattern recognition.

A special class of space-variant filters is the cascade of mapping plus space-invariant filtering. These provide a general paradigm for functional interpretations.

2.5 Reading List

Allman, J.M. & Kaas, J. H. (1971): Representation of the visual field in striate and adjoining cortex of the owl monkey (Aotus trivirgatus). *Brain Research*, **35**, 89-106.

Barlow, H. B. (1986): Why have multpile cortical areas? *Vision Research*, **26**, 81-90.

Knudsen, E. I., du Lac, S., Esterly, S. D. (1987): Computational maps in the brain. *Annual Review of Neuroscience*, **10**, 41-65.

Mallot, H. A. (1985): An overall description of retinotopic mapping in the cat's visual cortex areas 17, 18, and 19. *Biol. Cybern.* **52**: 45-51.

Mallot H. A. (1987): Point images, receptive fields, and retinotopic mapping. *Trends in Neurosci.* **10**: 310-311.

Schwartz, E. L. (1980): Computational anatomy and functional architecture of striate cortex: A spatial mapping approach to perceptual coding. *Vision Research*, **20**, 645-669.

Tusa, R. J., Rosenquist, A. C., Palmer, L. A. (1979): Retinotopic organization of areas 18 and 19 in the cat. *J. Comp. Neurol.*, **199**, 293 - 329.

van Essen, D. (1985): Functional organization of primate visual cortex. In: Peters, A. & Jones, E. G. (Eds.), *Cerebral Cortex, Vol. 3: Visual Cortex (pp. 259-329)*. New York and London: Plenum Press.

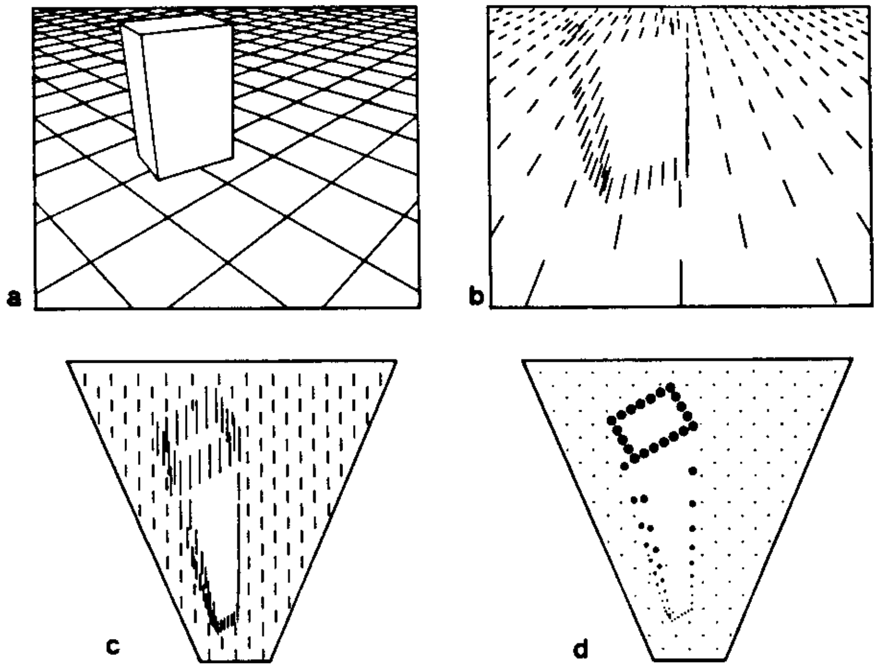

Figure 3: Optical flow analysis by topographic mapping. By inverting the perspective projection of the floor unto the image plane, the velocity vectors of elevated points can be detected. The method is robust against changes in elevation that are small as compared to the height of the observer (body-scale), i.e., pot-holes or bumps. *a.* Scene with obstacle. *b.* Needle-plot of the velocity field. *c.* Mapped velocity field. *d.* Detected obstacle.

3 Biological Strategies in Robot Navigation

3.1 Analysis of Biological Information Processing

Marr's three levels: computational theory, algorithms and representation, hardware implementation. Bottom-up inference (from the neural 'hardware' to the strategies of information processing) is possible in biologically evolved organisms due to *adaptation*. Structural adaptations occur on the architectural (rather than single cell) level, correspond to basic tasks in visual behavior, and can be identified by comparative anatomy. Cortical organization (see above). A preliminary list of structural principles of the (visual) cortex includes:

Architecture: layering, uniformity in the horizontal directions, mean dendritic and axonal arbors of pyramidal cells, positive distributed feedback.

Mapping: topographic mapping, patchy connections from left and right eye, columnar intrinsic organization.

From structural principles of these type, it should be possible to derive a *neural instruction set*, i.e., a set of basic operations that the brain uses in information processing. As an example, consider topographic mapping and uniform motion detection in optical flow analysis.

3.2 Obstacle Avoidance Based on Optical Flow Data

The optical flow generated by ego-motion in a plane. Inverse perspective mapping transform flow vectors of the ground plane into vectors of constant length and orientation (cf. Fig. 3). Comparison with complex logarithmic mapping. Body-scaled obstacle detection. Inverse perspective mapping and regularizing motion detection schemes. Motion detector: cf. Lecture by H. H. Bülthoff.

3.3 Zero-Disparity Mapping

Inverse perspective in stereopsis. Deformation of horoptor plane by topographic maps. Robotics implementation.

3.4 Discussion

Inverse Perspective Mapping in Biology: Representation of lower hemifield in the cat's area 17 compensates for perspective foreshortening.

Biological Information Processing

	Neural 'Computer'	Technical Computer
purpose	solve special problems	universal machine
representation & computation	isomorphic	arbitrary (symbolic)
number of computation steps	low	high

3.5 Reading List

Brooks, R. (1987): Autonomous mobile robots. In: W. E. L. Grimson & R. S. Patil (eds.) *AI in the 1980s and beyond*. Cambridge, Mass. (MIT Press).

Epstein, L. I. (1984) An attempt to explain the differences between the upper and lower halves of the striate cortical map in the cat's field of view. *Biol. Cybern.* **49**: 175-177.

Jain, R., Barlett, S. L., O'Brien, N. (1987): Motion stereo using ego-motion complex logarithmic mapping. *IEEE Trans. Pattern Anal. Machine Intel.* **PAMI-9**: 356-369.

Mallot, H. A., Schulze, E., Storjohann, K. (1988): Neural network strategies for robot navigation. In: Dreyfus, G. & Personnaz, L. (Eds.), *Proceedings nEuro-88*, in press.

Mallot, H. A., von Seelen, W. (1988): Why cortices? Neural networks for visual information processing. In: J.-P. Ewert & M. A. Arbib (eds.) *Visuomotor integration: Amphibians, comparisons, models, and robots*. New York (Plenum Press), in press.