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**SEMMELWEIS
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Development of Complex Curricula for Molecular Bionics and Infobionics Programs within a consortial* framework**

Consortium leader

PETER PAZMANY CATHOLIC UNIVERSITY

Consortium members

SEMMELWEIS UNIVERSITY, DIALOG CAMPUS PUBLISHER

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BEVEZETÉS A FUNKCIONÁLIS NEUROBIOLÓGIÁBA

INTRODUCTION TO FUNCTIONAL NEUROBIOLOGY

By Imre Kalló

Contributed by: Tamás Freund, Zsolt Liposits, Zoltán Nusser, László Acsády, Szabolcs Káli, József Haller, Zsófia Maglóczky, Nórbert Hájos, Emilia Madarász, György Karmos, Miklós Palkovits, Anita Kamondi, Lóránd Eröss, Róbert Gábrriel, Kisvárdai Zoltán

Visual Processing

Imre Kalló & Zoltán Kisvárday

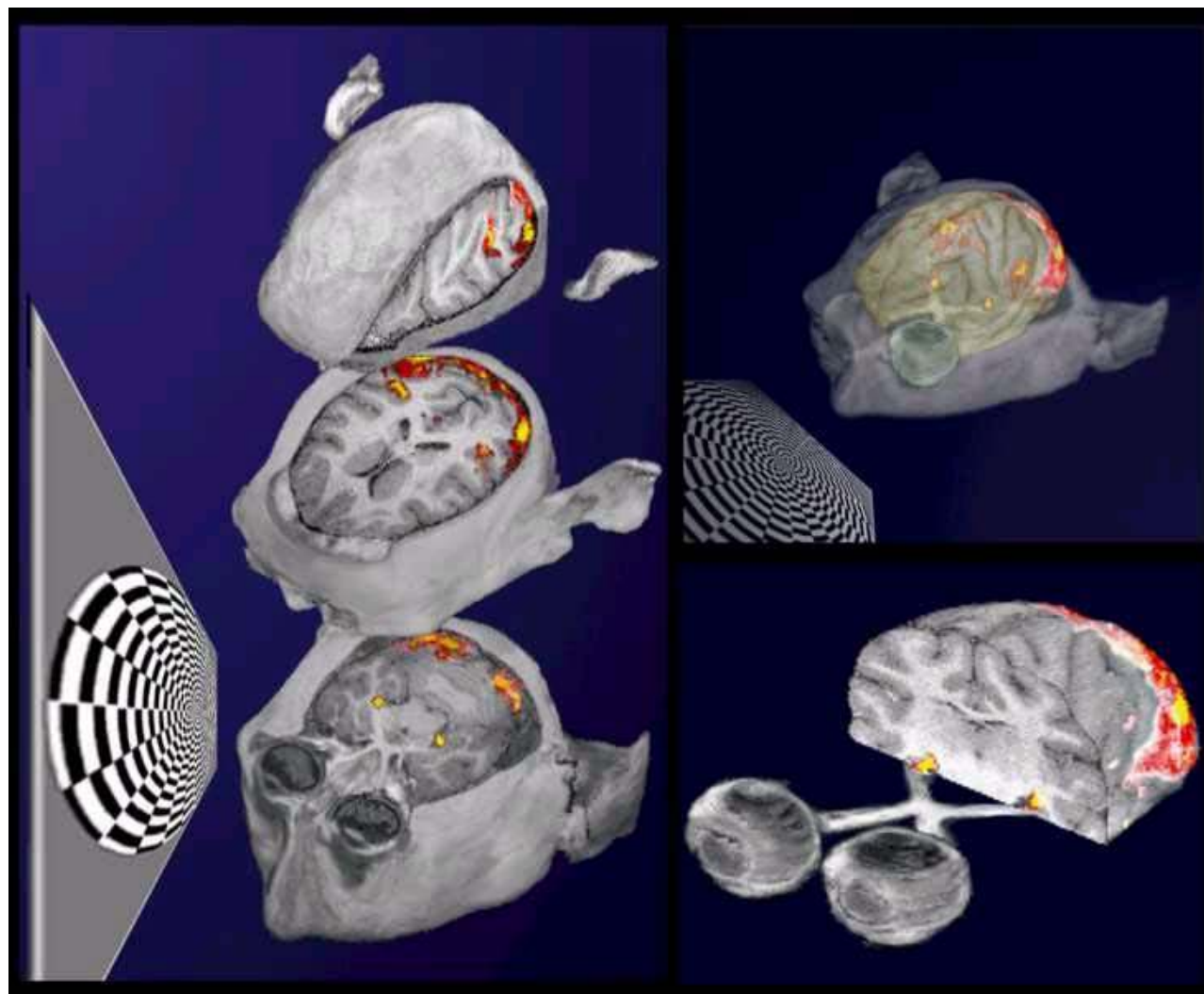
Pázmány Péter Catholic University, Faculty of Information Technology

- I. Visual pathway and processing movement, color and contour information in the human brain.
- II. Structure and function of the visual cortex.
- III. The receptive field. Functional studies on the orientation and direction selectivity.

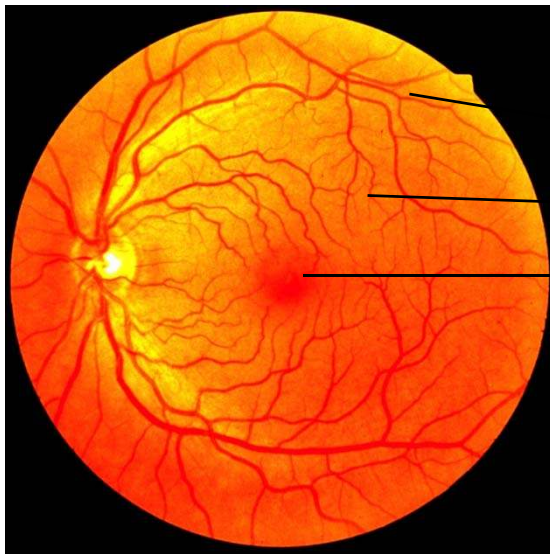
I. Visual pathway and processing movement, color and contour information in the human brain.

Exp: Development of imaging techniques greatly facilitated the studies on the central processing of movement, color and contour information. A monkey while observing a specific circular pattern of alternating black and white squares was investigated using functional magnetic resonance imaging (fMRI). This revealed bilateral activated areas in the brain along the visual pathway i.e. the lateral geniculate body and visual cortical areas, as both sides of the brain receive information from the visual field.

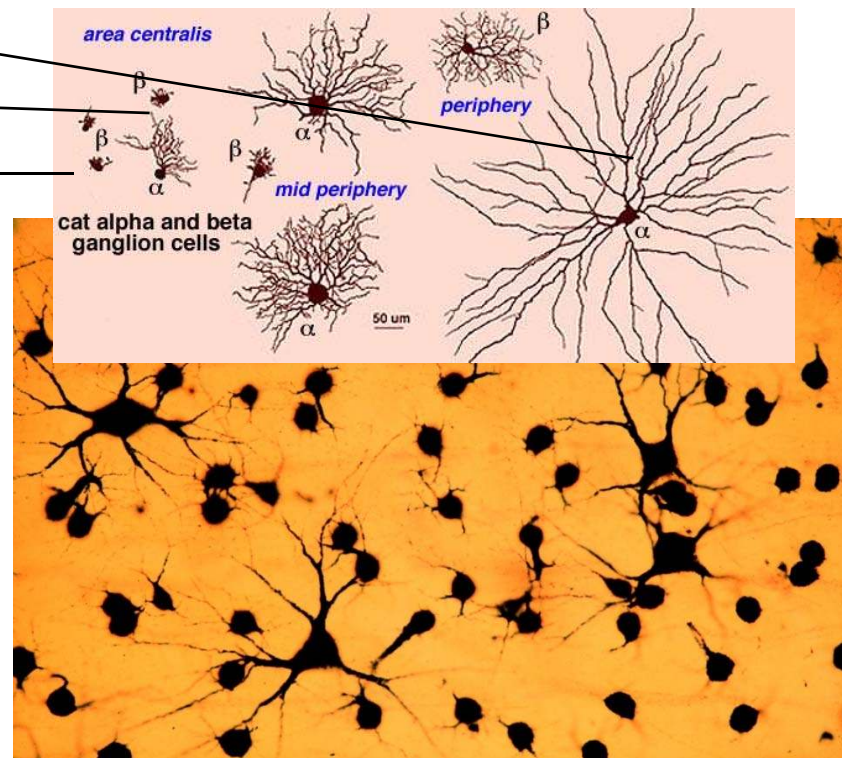
Basics of processing of the movement, colour and contour information



M (magno, parasol, Y) and **P** (parvo, midget, X) neurons form functionally different pathways towards the visual centers of the brain



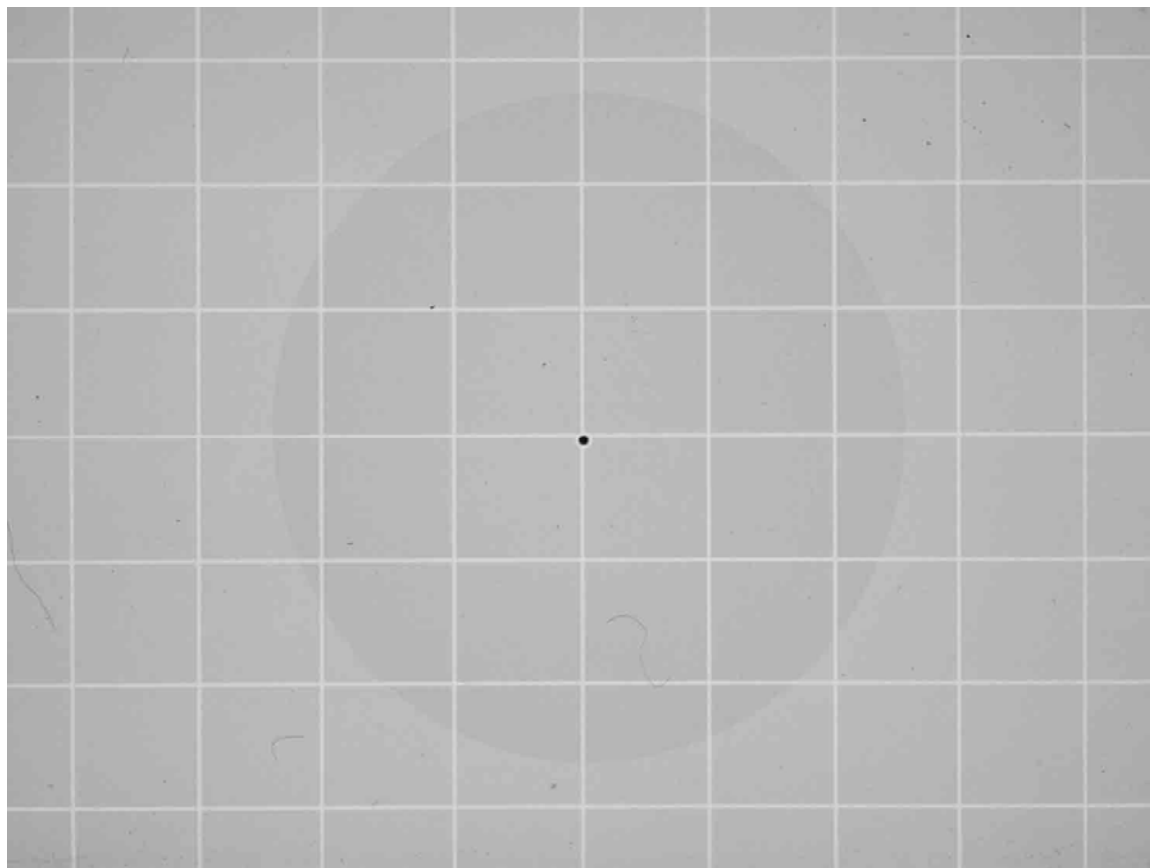
Types of ganglion cells



Activity pattern

Magno	-	phasic
Parvo	-	tonic

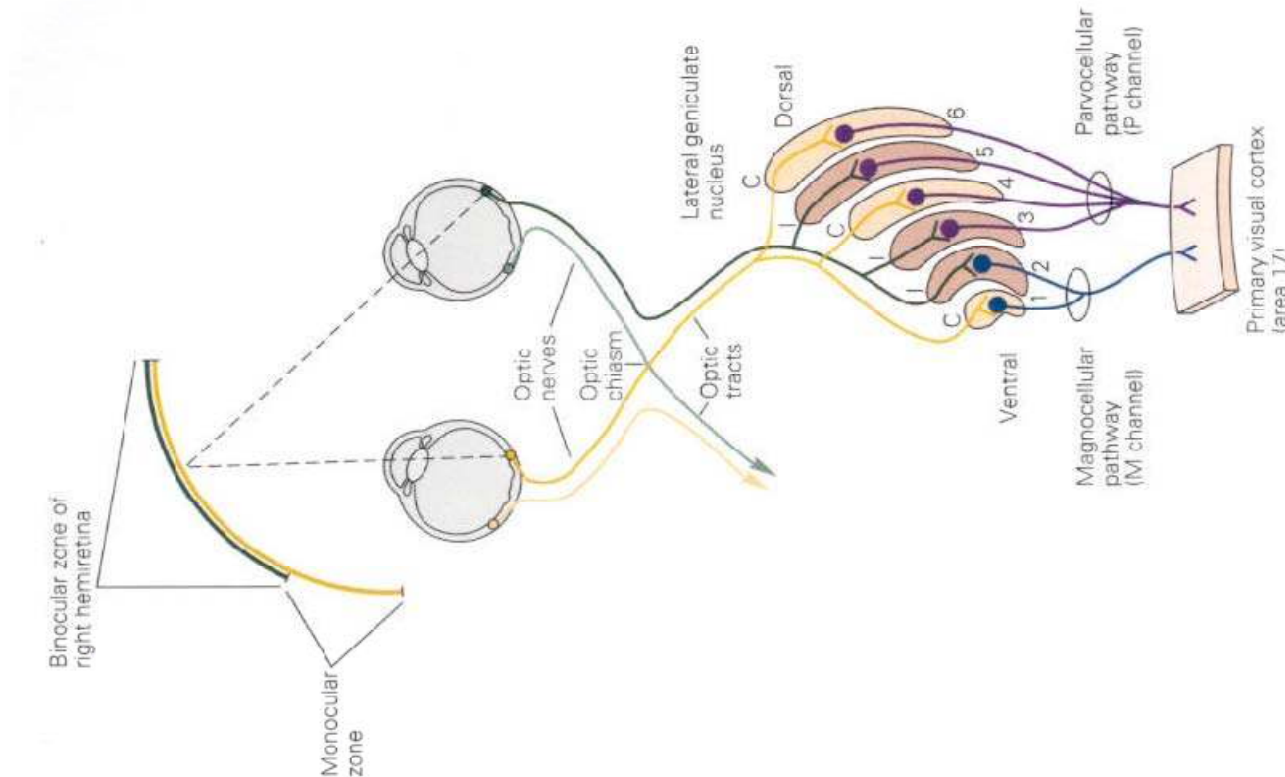
Parvo-cells can see the mesh
Magno-cells can see the low-contrast circle



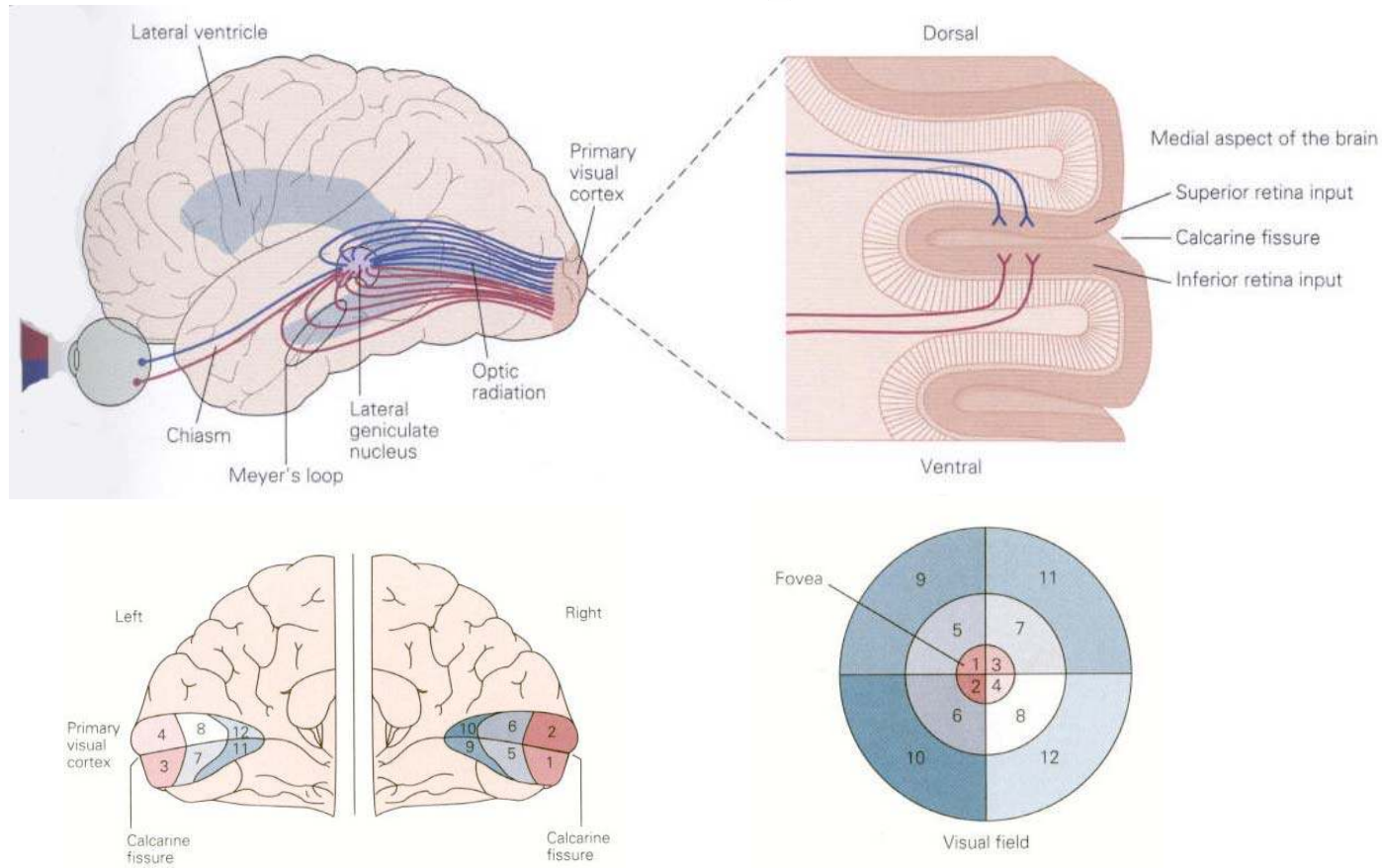
Magno-cells participate also in shape-recognition



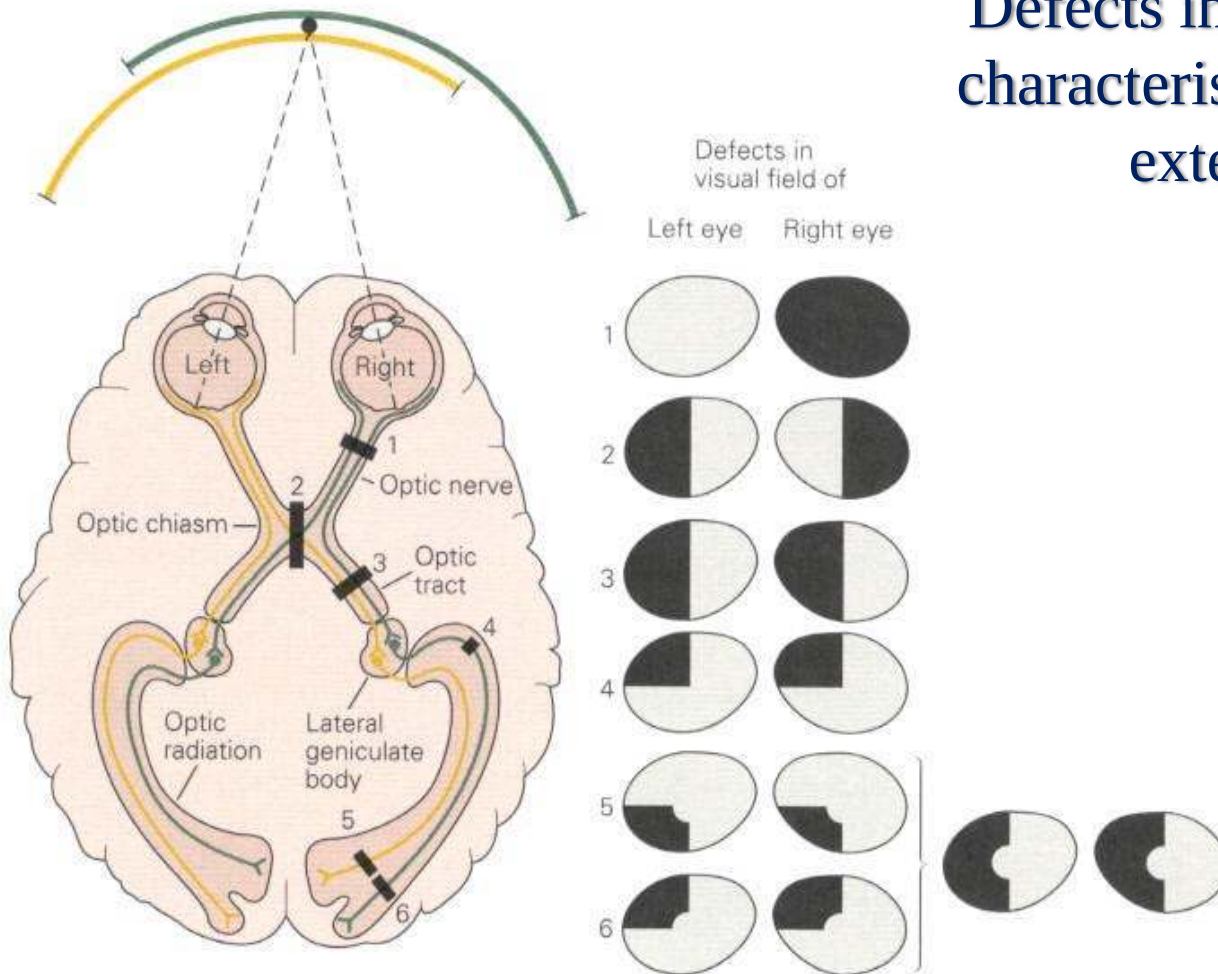
Fibers of Magno- and Parvo cells are relayed in the visual-thalamus (dLGN) towards Area17 (V1)

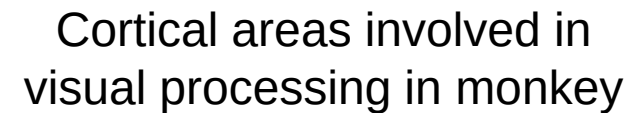


Projection of visual information to the visual cortex (V1) is retinotopic

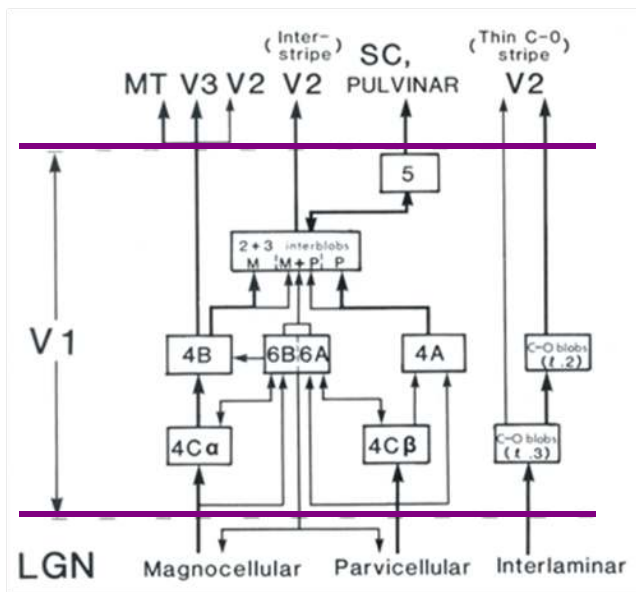


Defects in the visual field is characteristic for the site and extent of injury

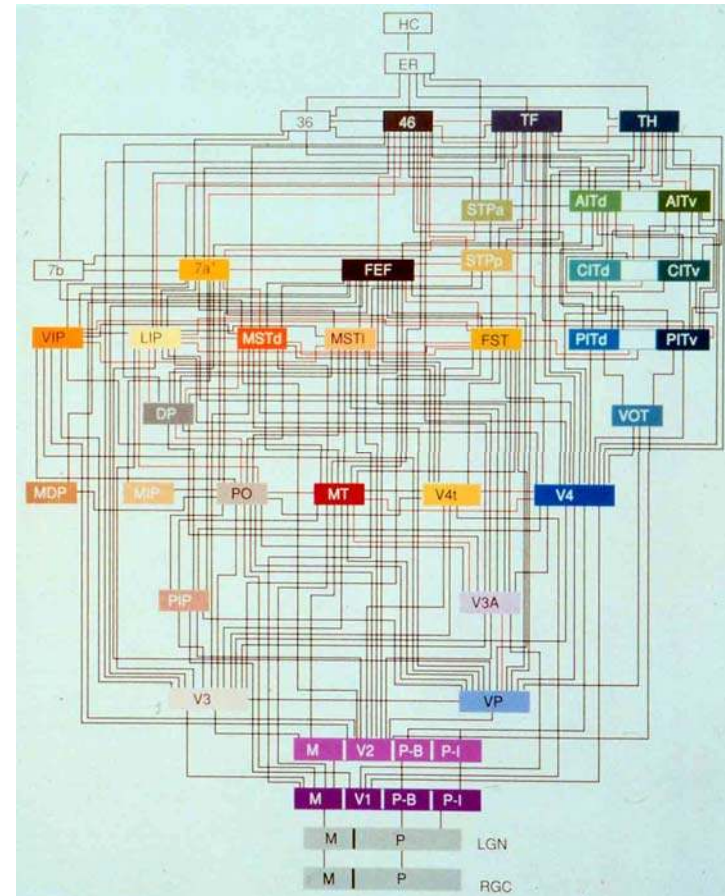




Hierarchic wiring of visual cortical areas



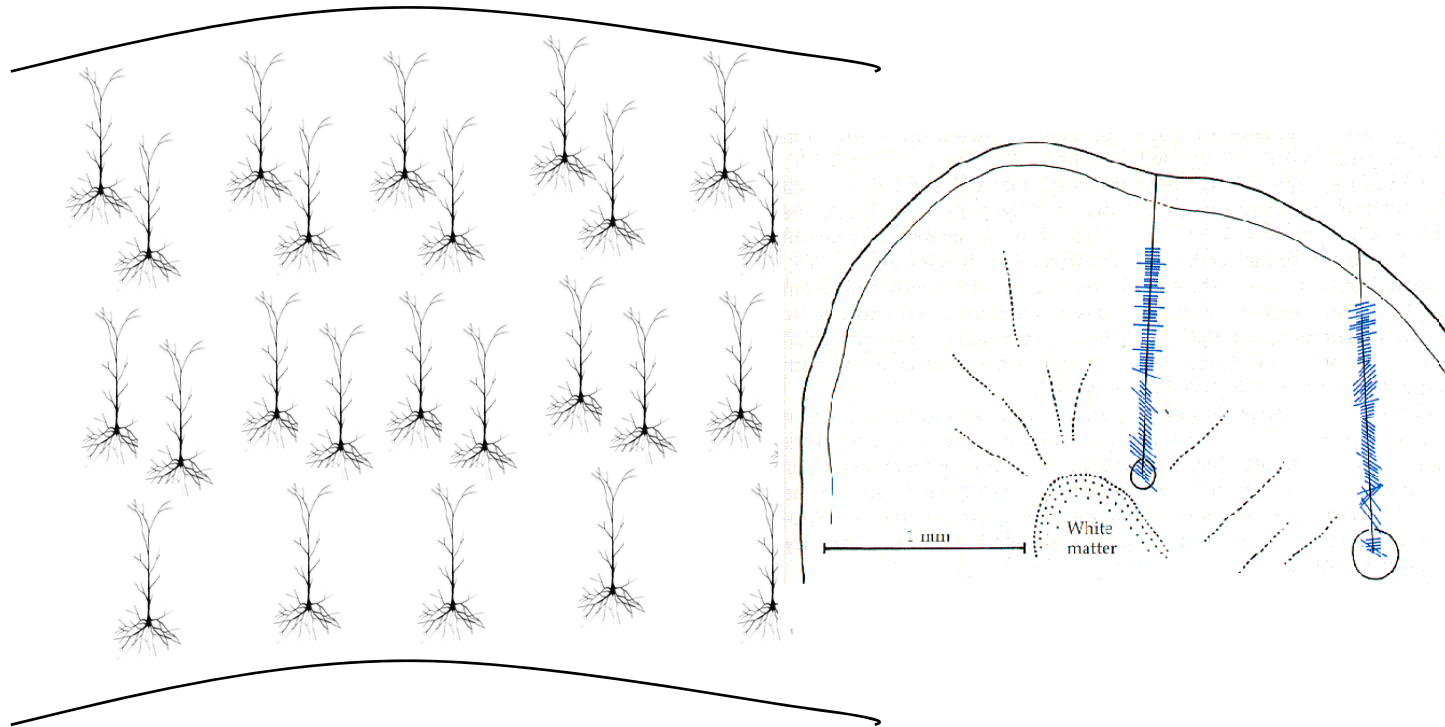
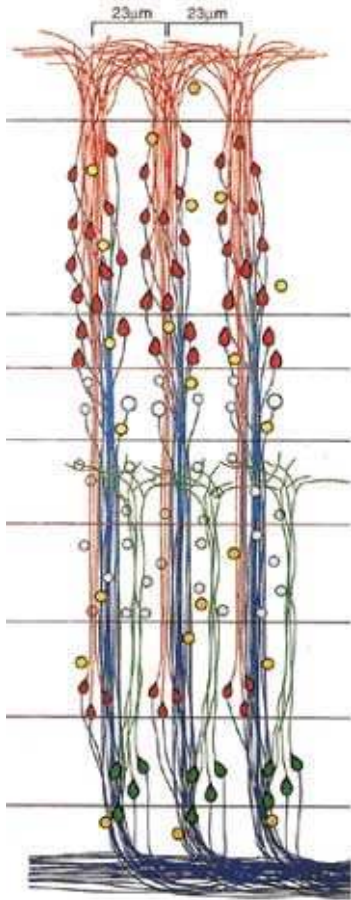
1985



1991

(Felleman and Van Essen, 1991)

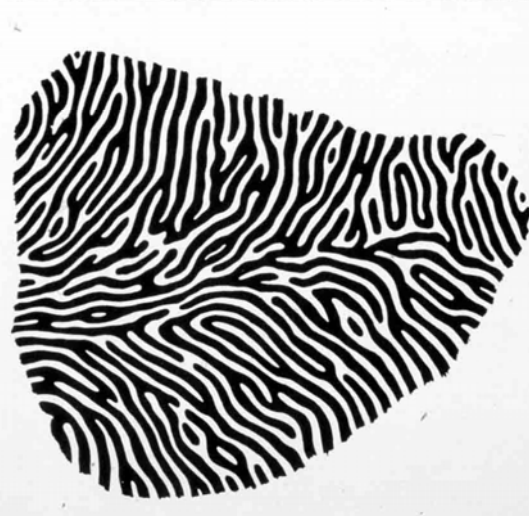
The cerebral cortex „is built” from columnar structures (morphological and functional units)



There are columns of eyedominance in the visual cortex of both monkeys and humans



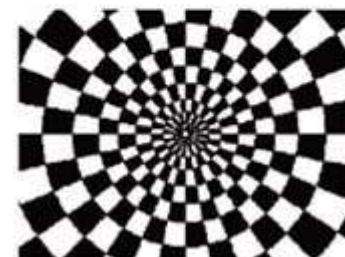
(monkey
2-deoxyglucose
labelling)



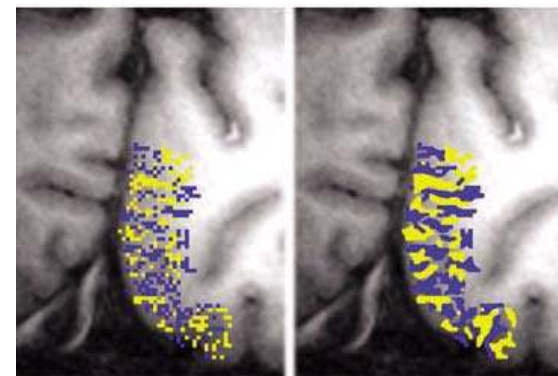
(human, fMRI)

 Left eye > Right eye

 Right eye > Left eye

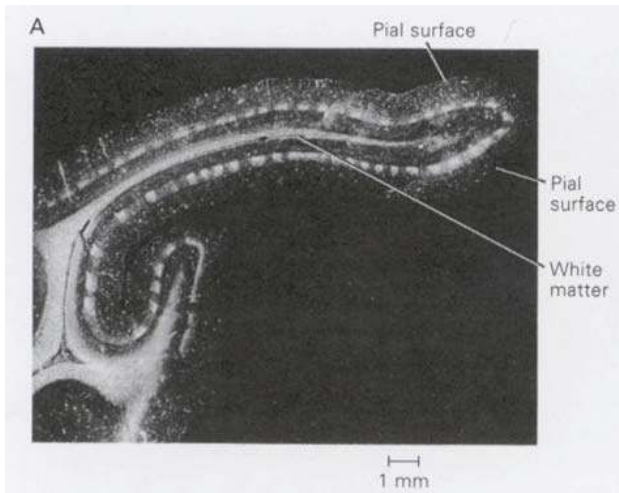
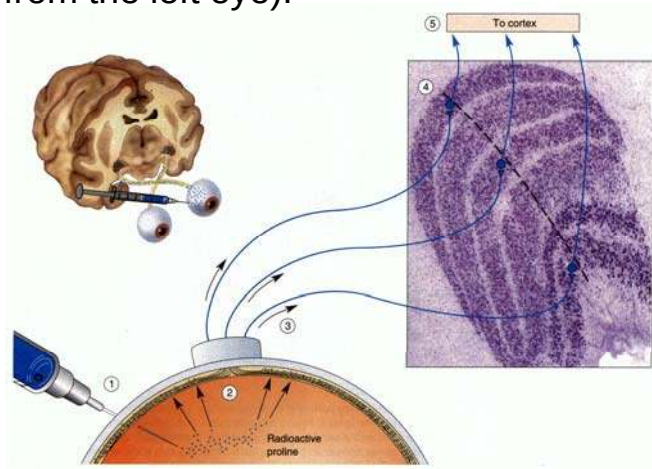


Stimulus

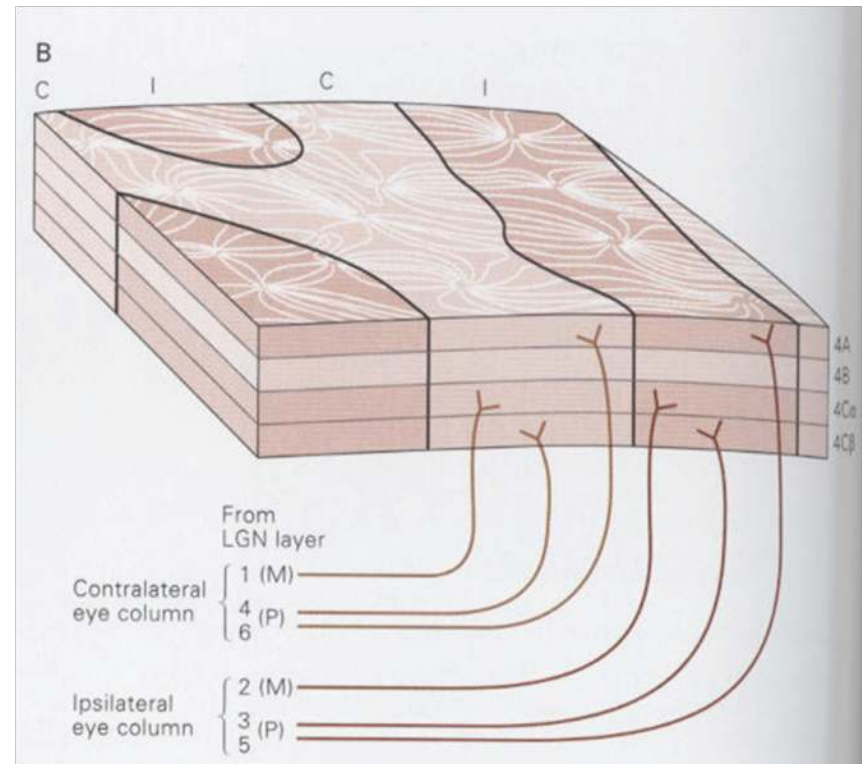


1 cm

Trans-synaptic tracing (^3H -amino acids, e.g. ^3H -leucine uptake from the left eye).



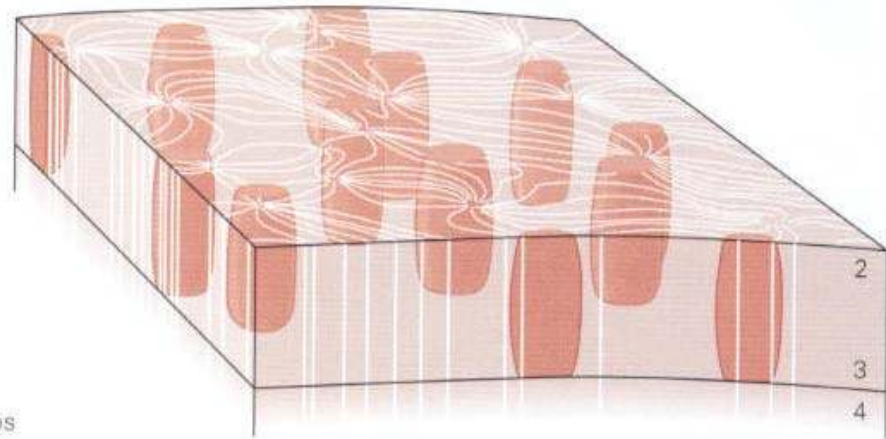
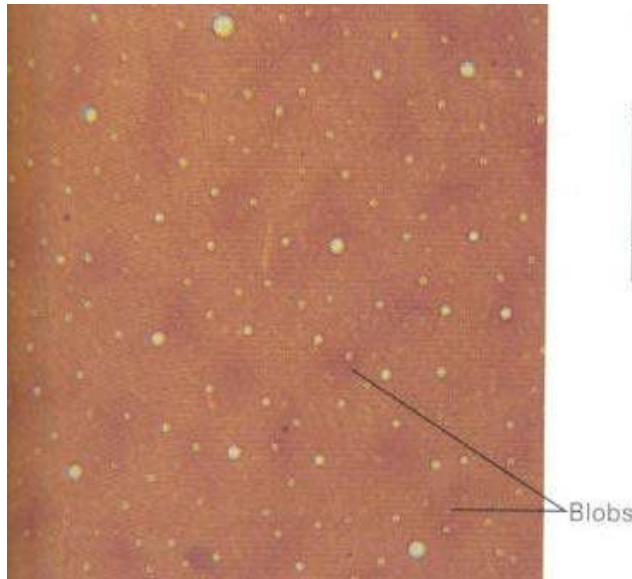
Demonstration of columns of eyedominance in the visual cortex of monkey



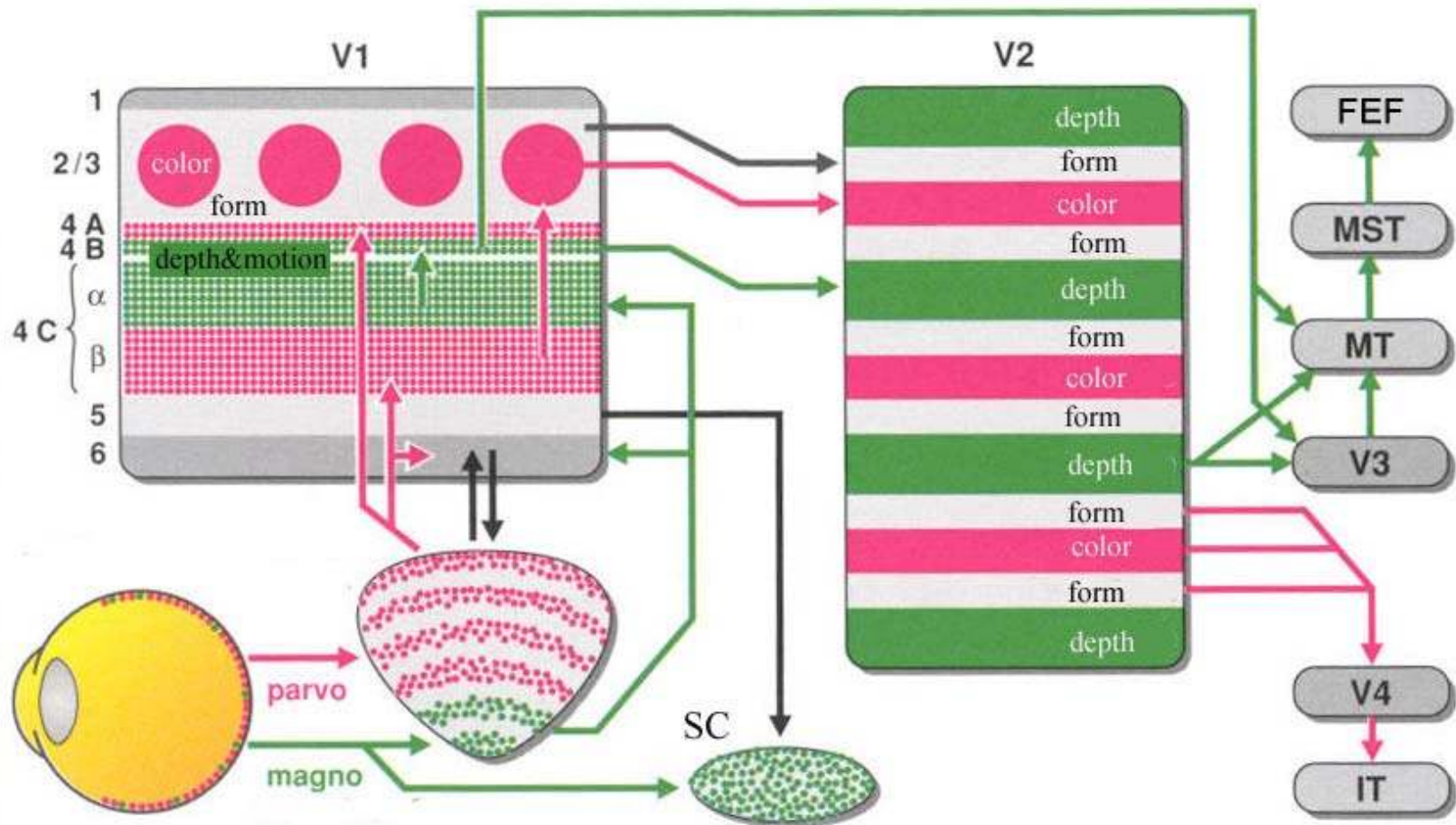
Cytochrome-oxidase positive columns („blobs”) in the visual cortex of the monkey (V1).



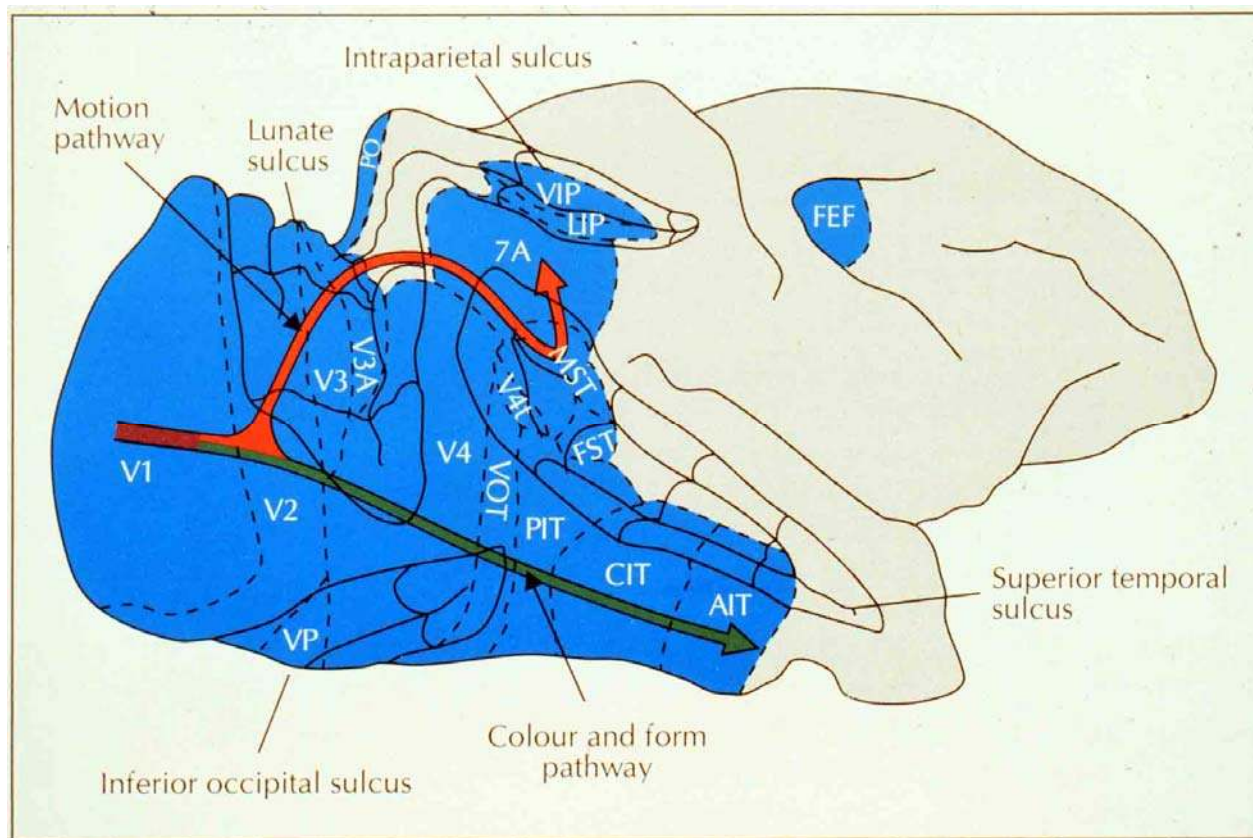
Its function is unknown.... but it marks a group of colour-sensitive cells.



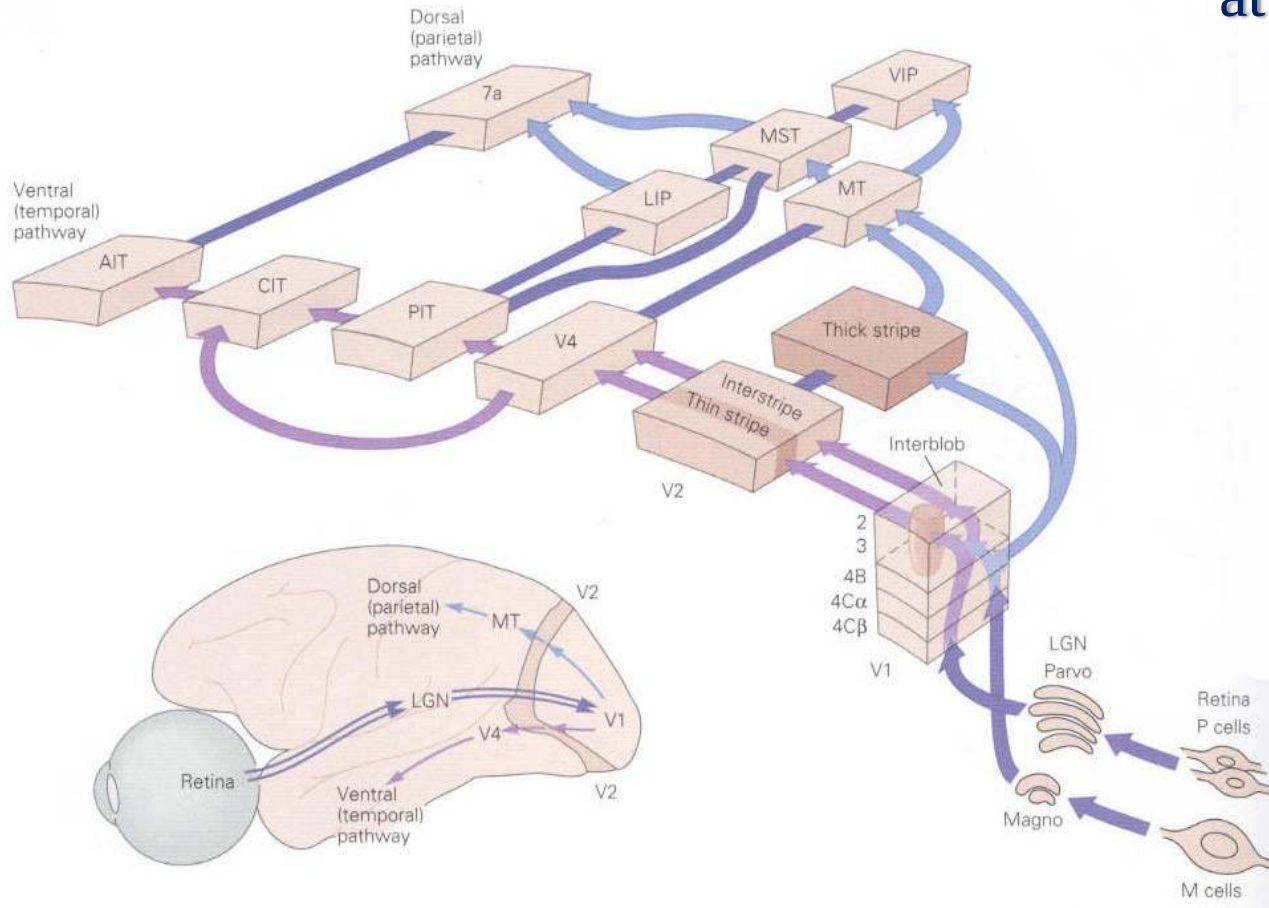
Cortical connections of Magno- and Parvo-pathways



Temporal and parietal cortical pathways „what” vs. „where” – perception vs. action



The dorsal and ventral pathways communicate with each other at multiple levels



Functional characteristics of the cells in the V1, V2, V3, V4 and MT areas



perception of colours

shape recognition

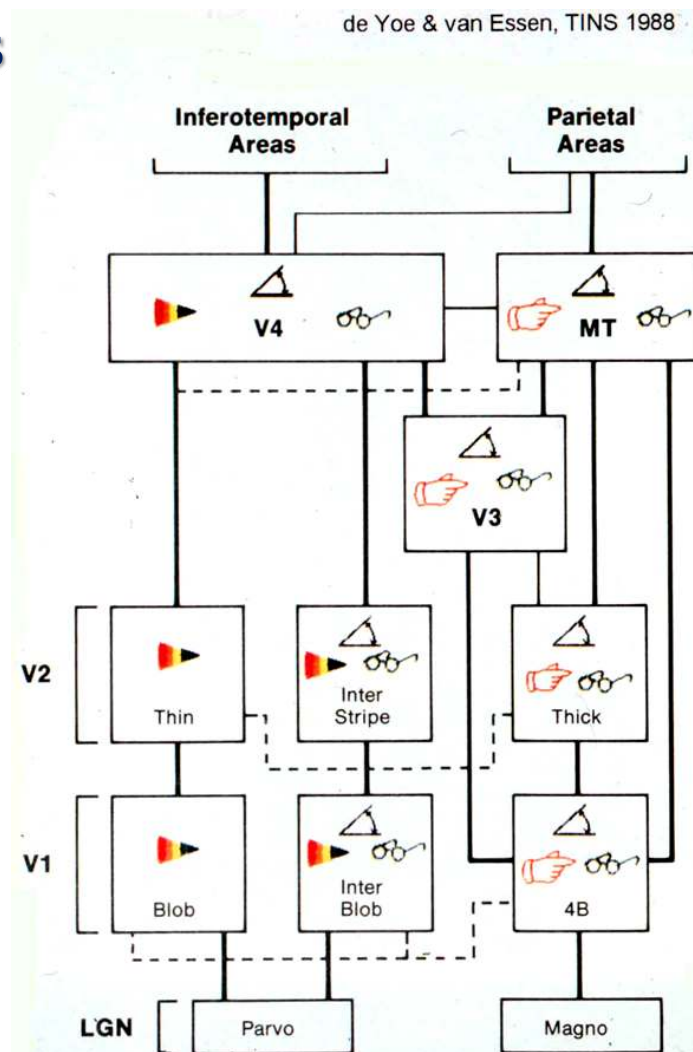
perception of movement

stereovision

deYoe & van Essen, TINS 1988

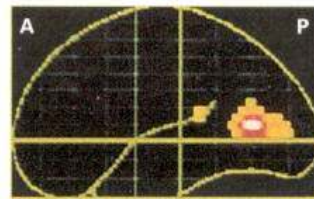
TABLE I. Neuronal selectivities of visual areas in the macaque^a

P-B stream	P-I stream	M stream
		V4
		WVL 50
		DIR 5
		ORI 50
		DIS 40
		V3
		WVL 15
		DIR 40
		ORI 70
		DIS 40
V2 thin	V2 inter	V2 thick
WVL 85	WVL 65(-)	WVL 15
DIR 5	DIR 0	DIR 20
ORI 20(-)	ORI 20	ORI 50
DIS 30(-)	DIS 20	DIS 70
V1 blob	V1 inter	V1 4B
WVL 65	WVL 40	WVL 10
DIR -	DIR -	DIR 50
ORI -	ORI ++	ORI 85
DIS?	DIS ++	DIS +

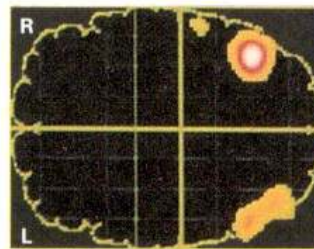


Colour and movement stimulate different cortical areas

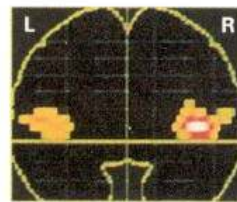
Motion study:
moving vs. stationary



Sagittal



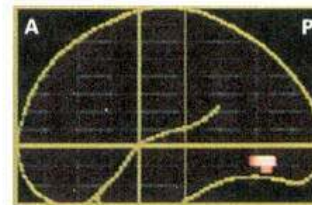
Transverse



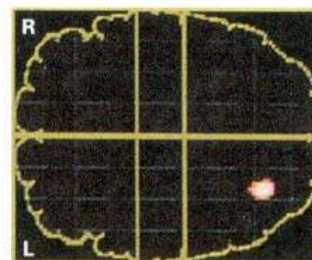
Coronal

Motion Area

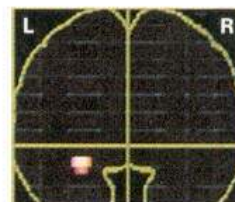
Color study:
color vs. gray



Sagittal



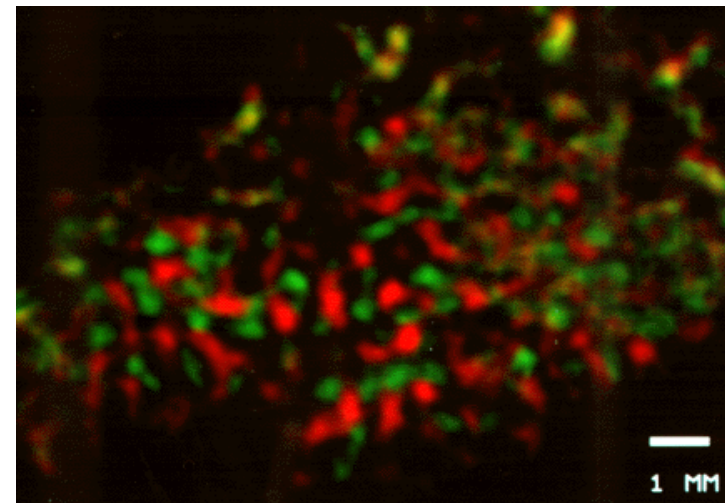
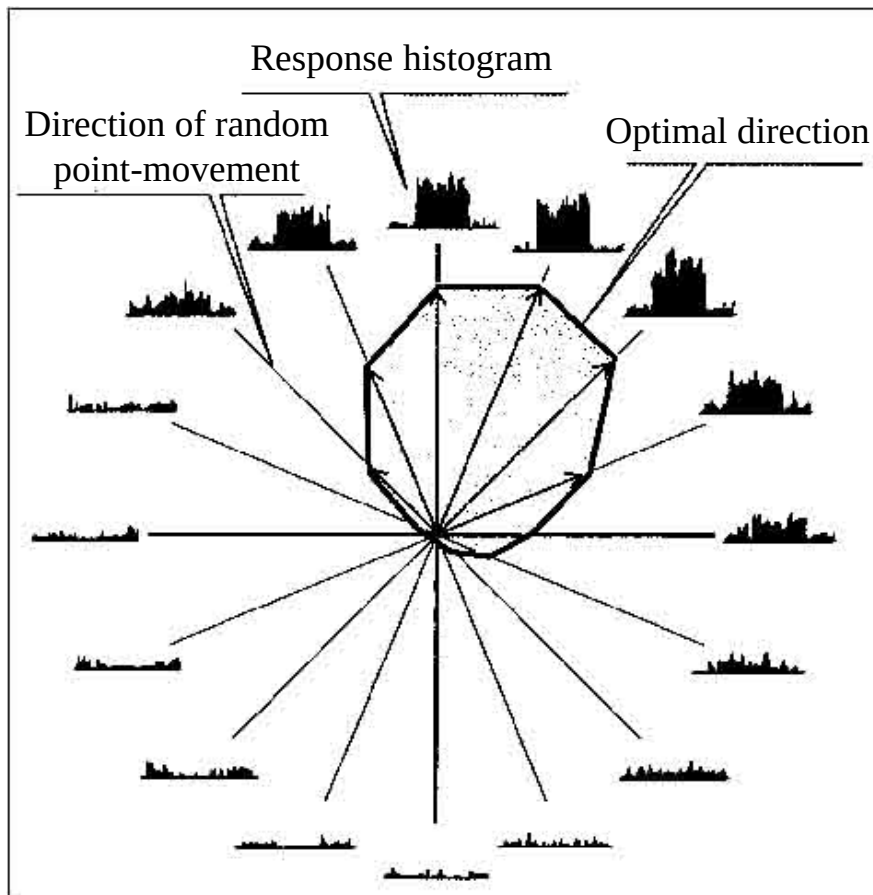
Transverse



Coronal

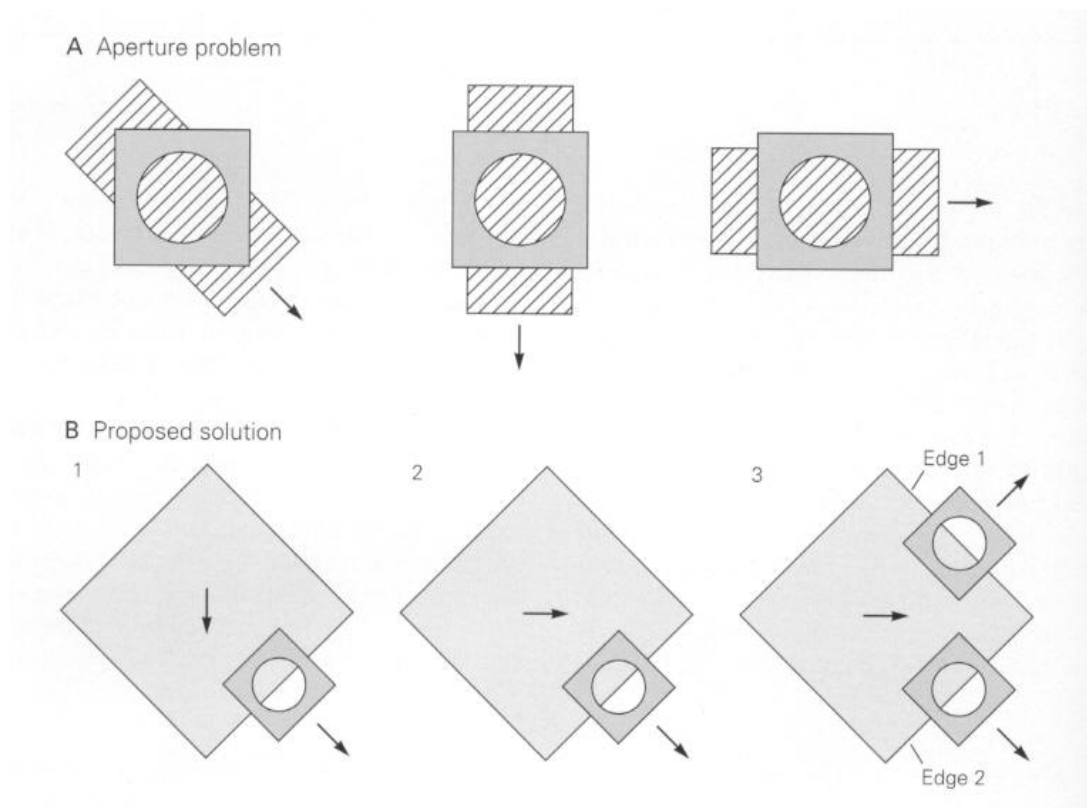
Inferior-medial area of
the occipital cortex

Neurons in the MT (V5) are motion-sensitive



(Tootell, Born & Hamilton 1988)

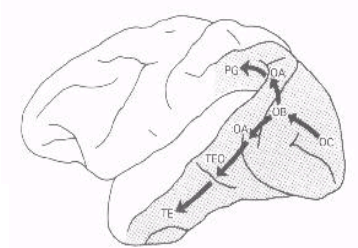
The aperture-problem



Cells at lower levels of hierarchy carry out „simple” image processing and transfer the result to cells at higher levels of hierarchy (V1-V5-MST...).

Aperture-problem is solved by MT cells

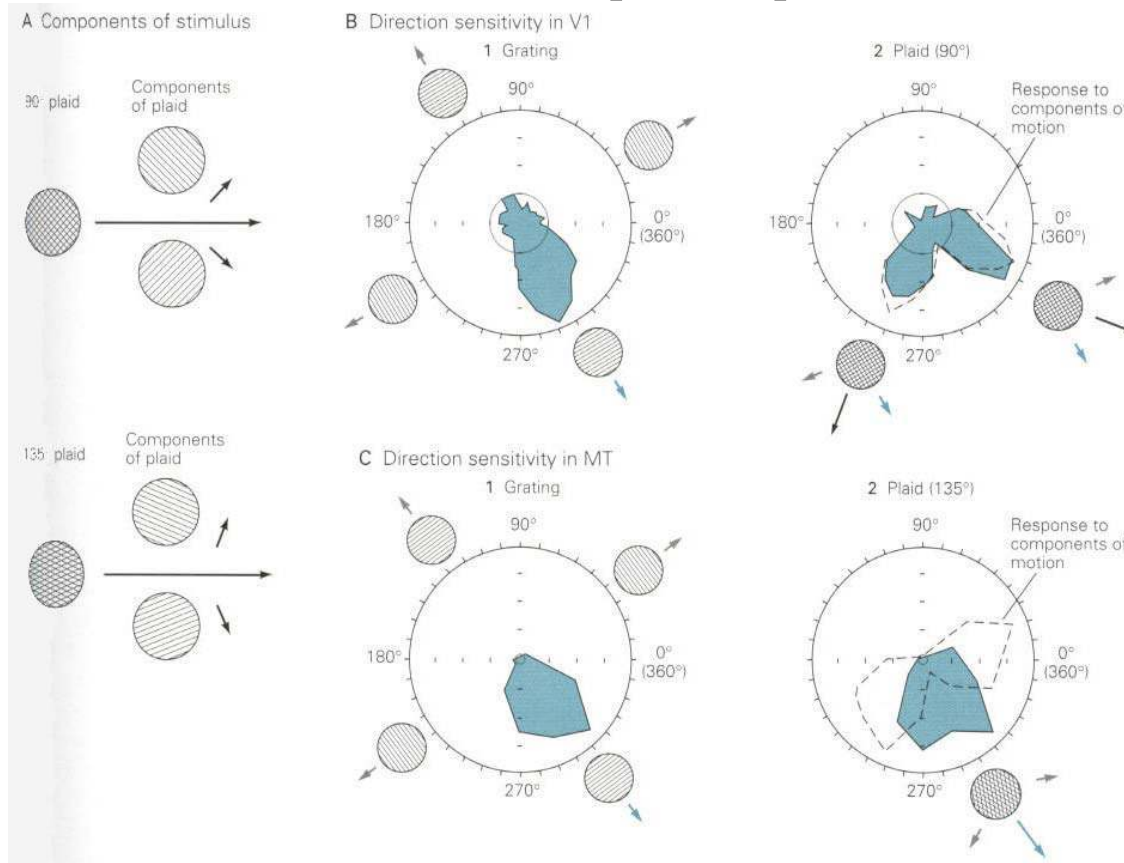
The RF of V1 cells is small → aperture problem



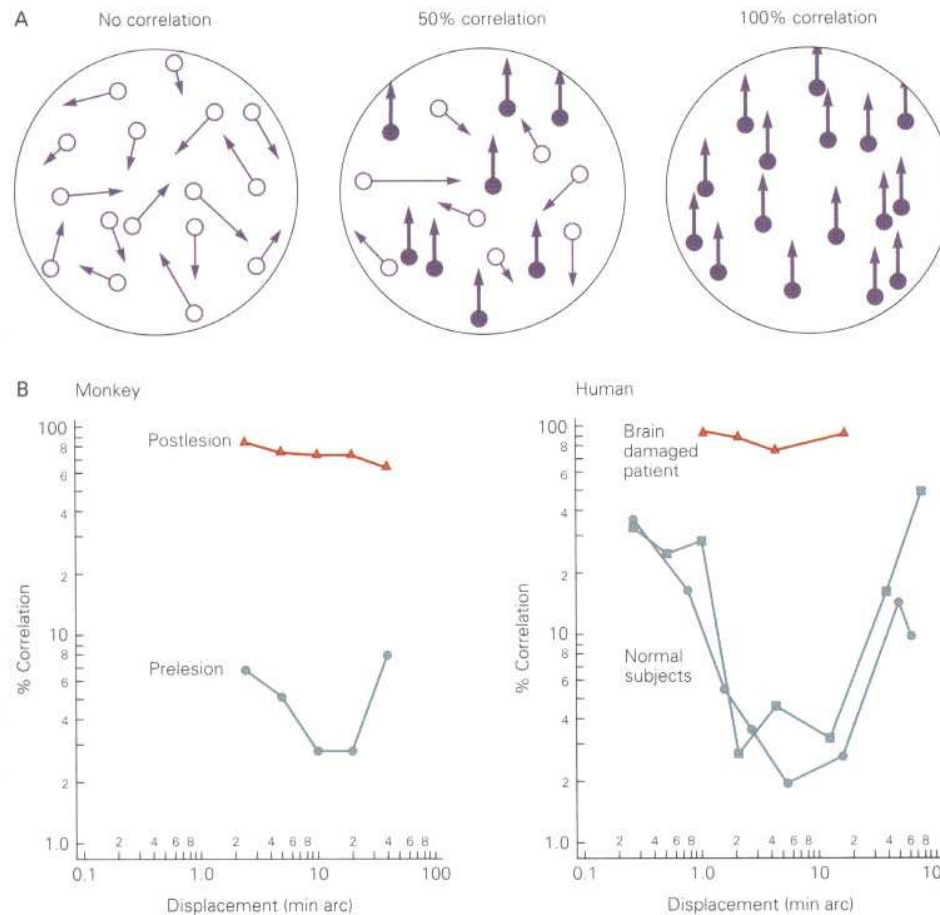
(Mishkin et al., 1983)

V1

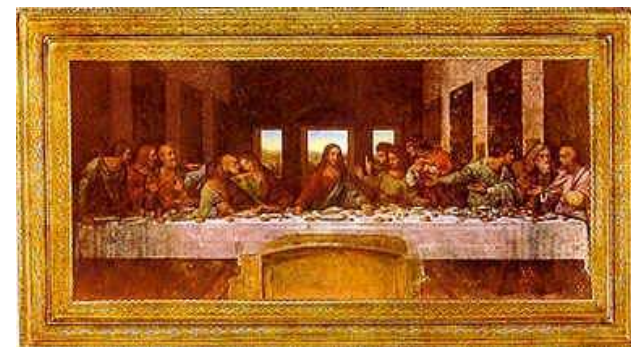
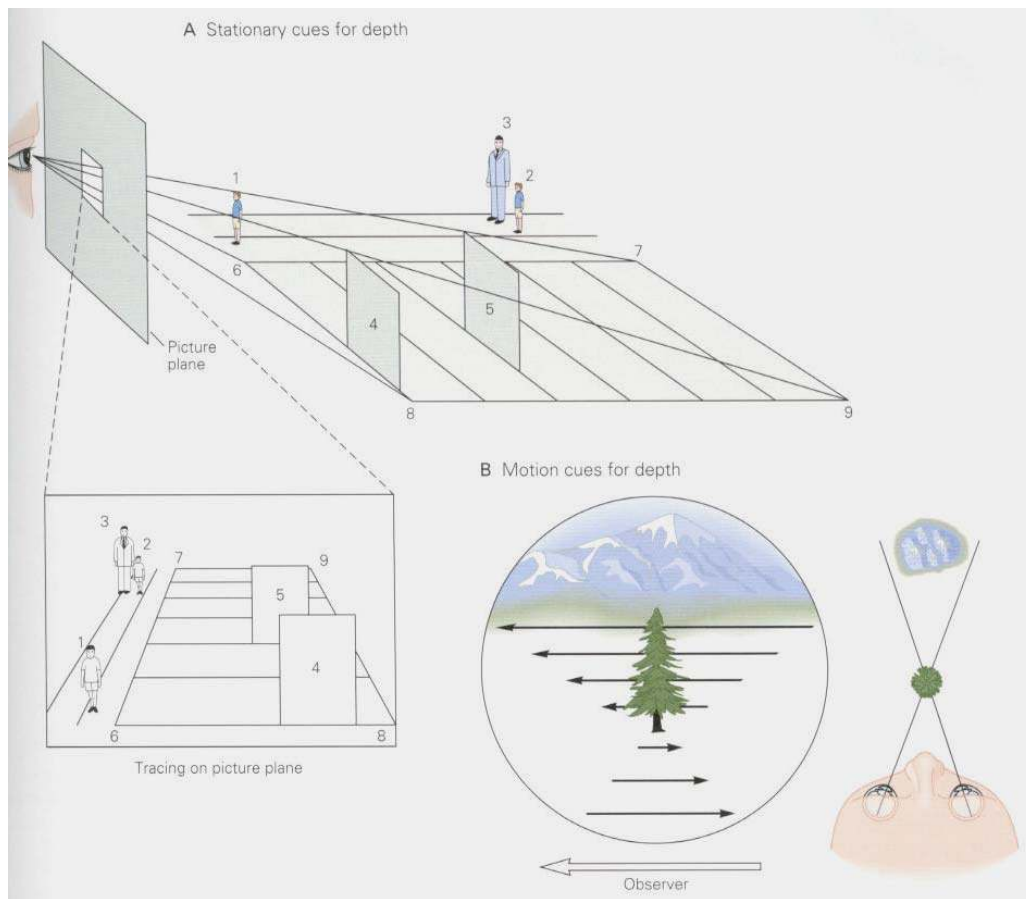
MT(V5)



Lesion of MT (V5) results in disturbance in motion perception



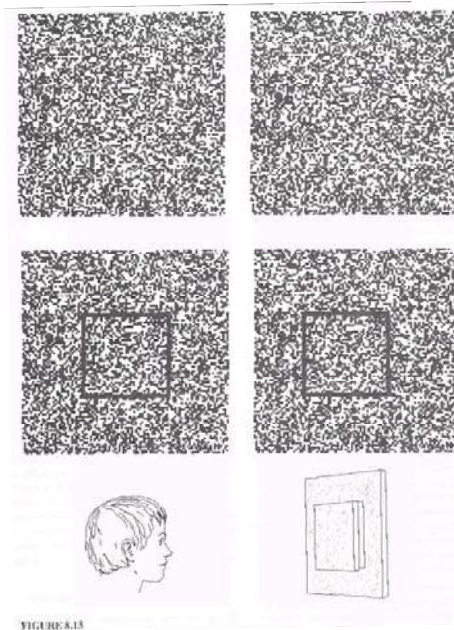
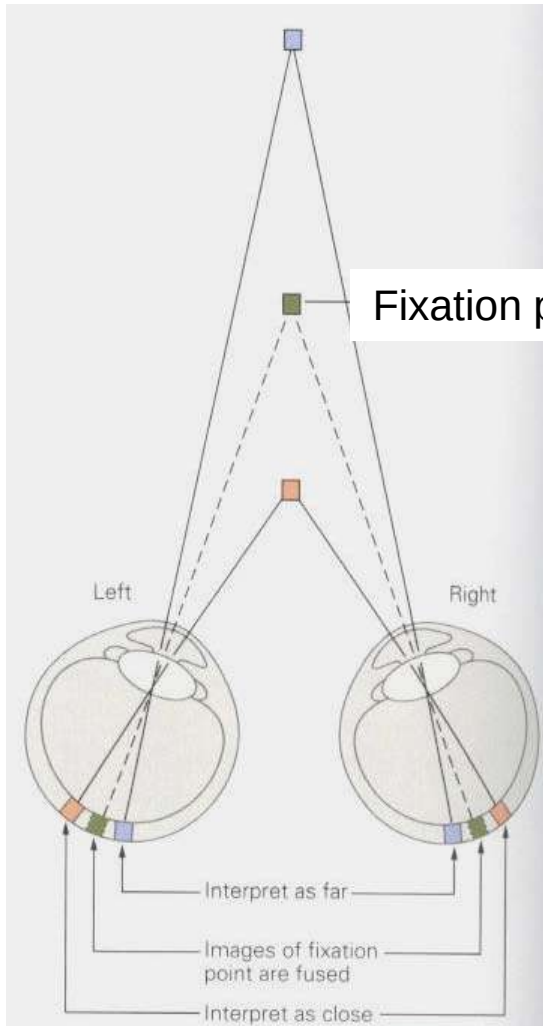
Factors determining monocular (far-field) depth vision (>30 m)



- known dimension (2,3)
- overlaying (4,5)
- linear perspective (6-7,8-9)
- dimensional perspective (1,2)
- tone (lighter is nearer)
- movement parallax !!
near object: fast and opposite direction
far object: slow and same direction

Factors determining binocular (near-field) stereoscopic vision (<30 m)

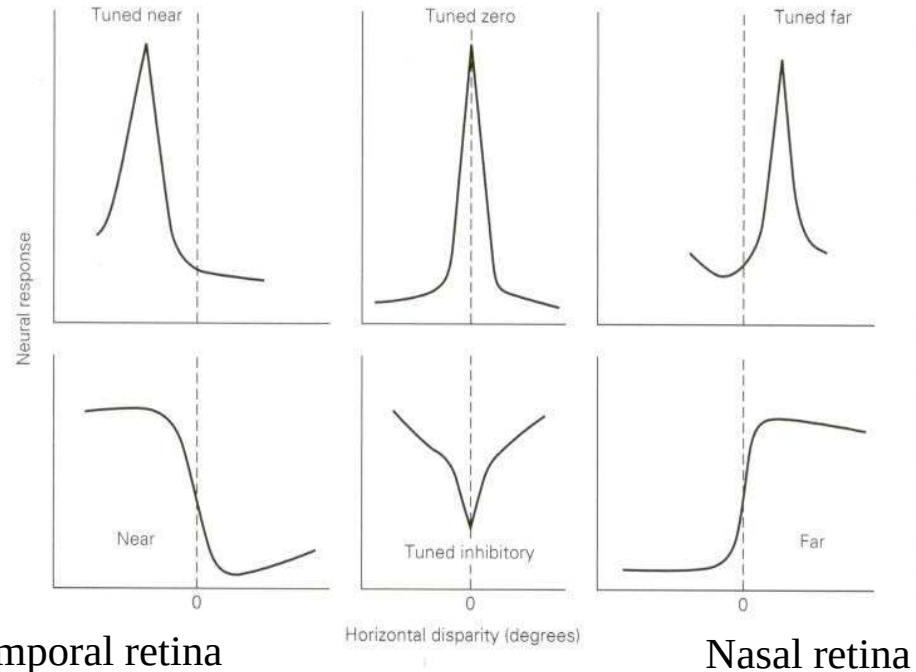
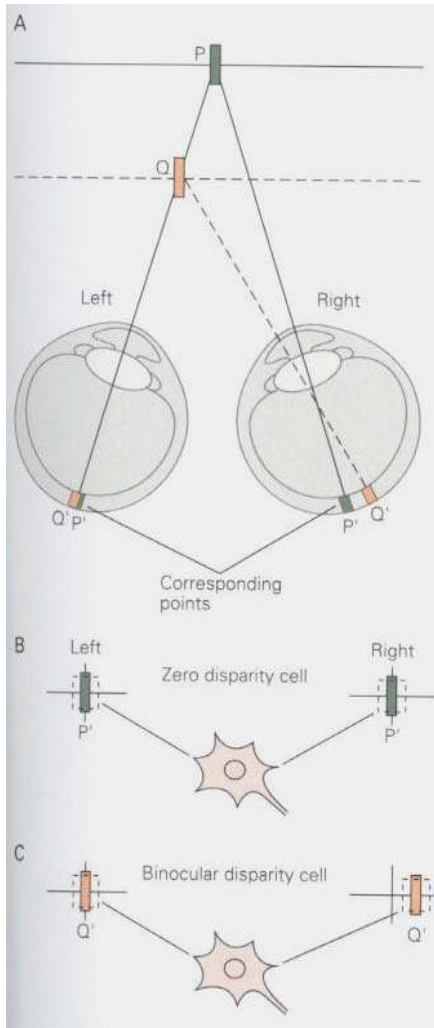
Identical points of 3D objects are projected to different (non-corresponding) points of the retina (binocular disparity).



What is primary, object- or stereo-recognition?

Stereo-recognition appears already in V1 (Béla Julesz)

Depth- (disparity) sensitive cells (MST)

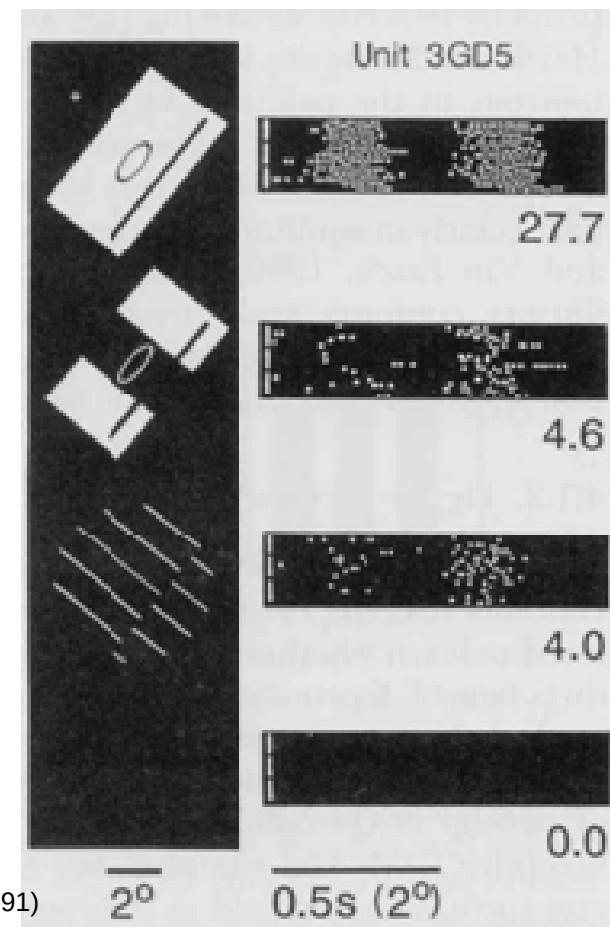
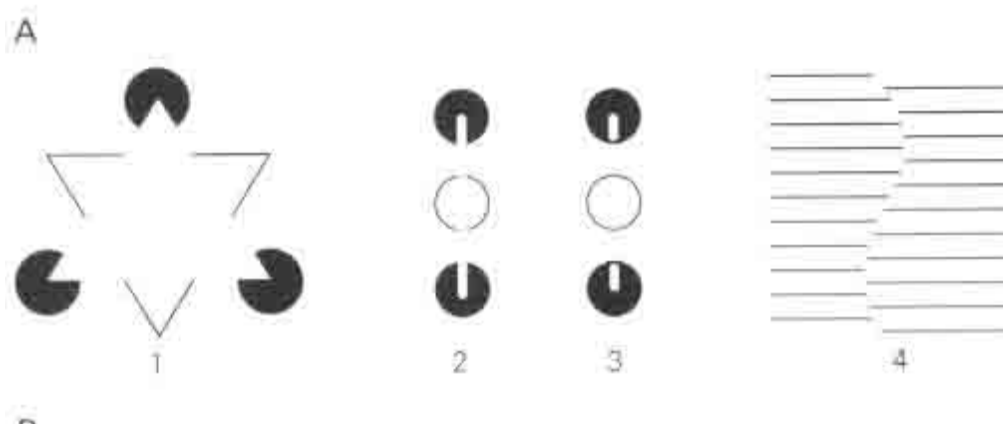


Temporal retina

Nasal retina

- V1 - Magno-pathway
- V2 - "thick" CO band
- MT - motion-selective cells
- MST - „near-far” cells

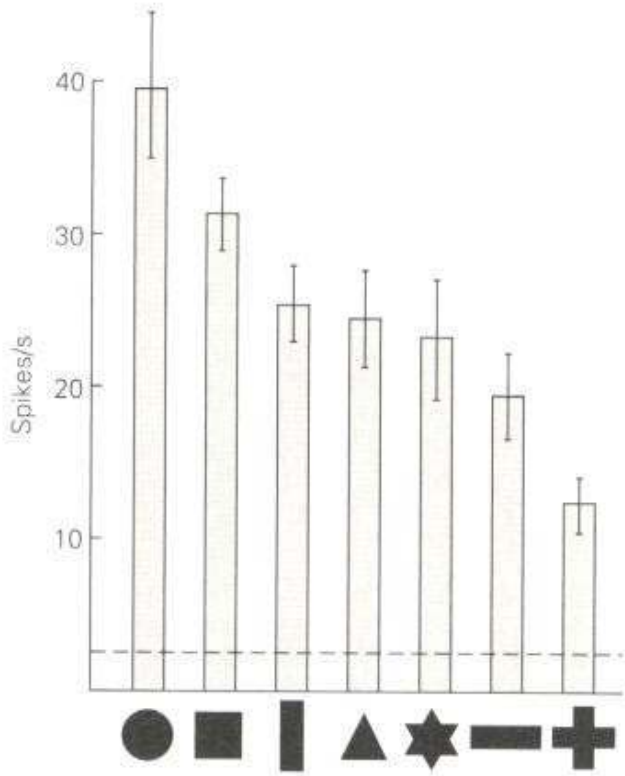
V2 (V1) cells can detect illusory contours



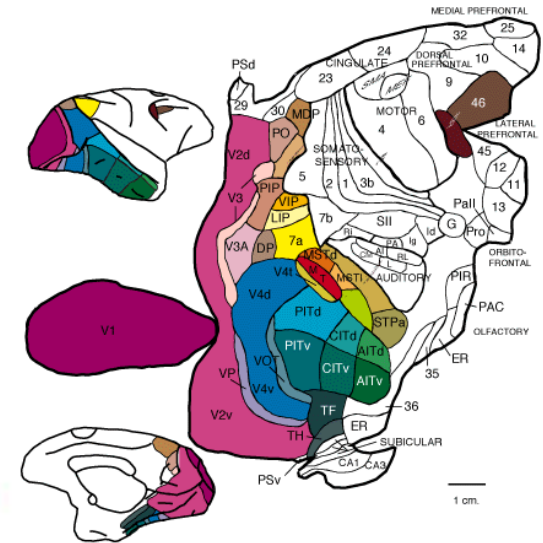
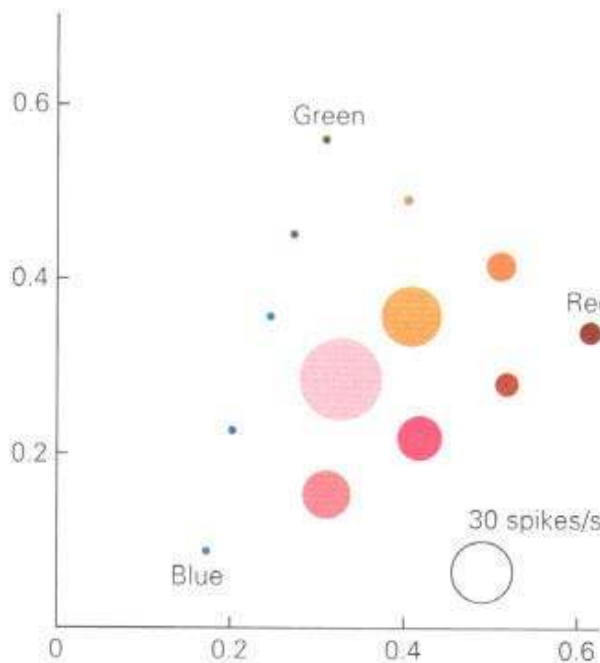
(Peterhans and von der Heydt, 1991)

IT (Inferior Temporal Area) cells detect shape- and colour differences

A Shape selectivity



B Color selectivity

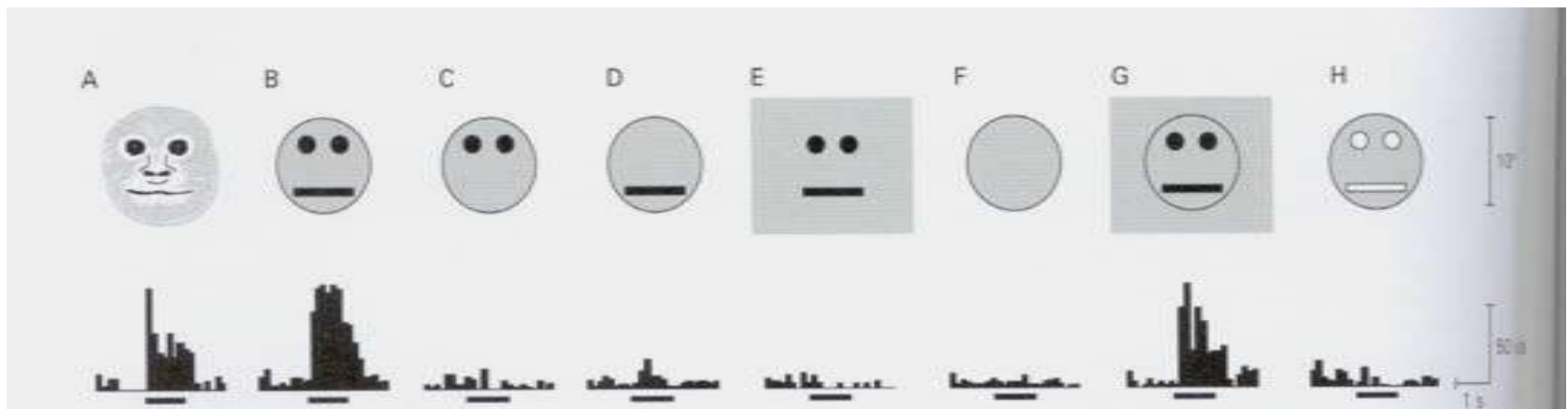
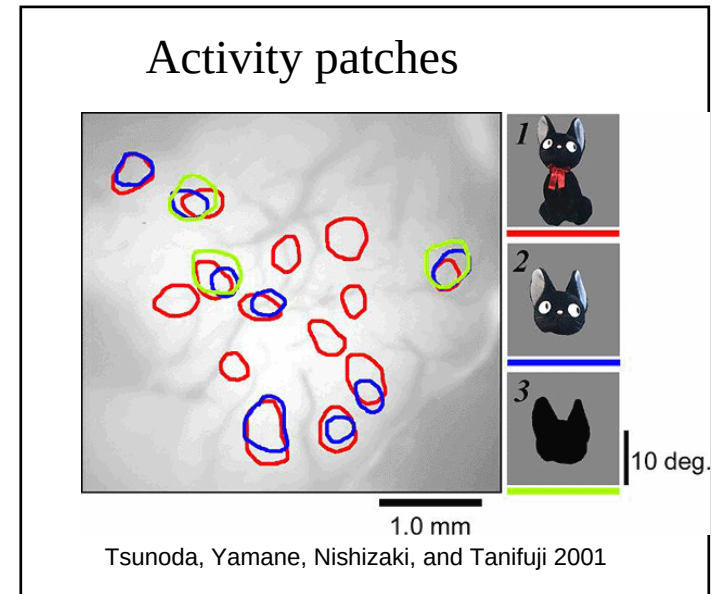


(Felleman and Van Essen, 1999)

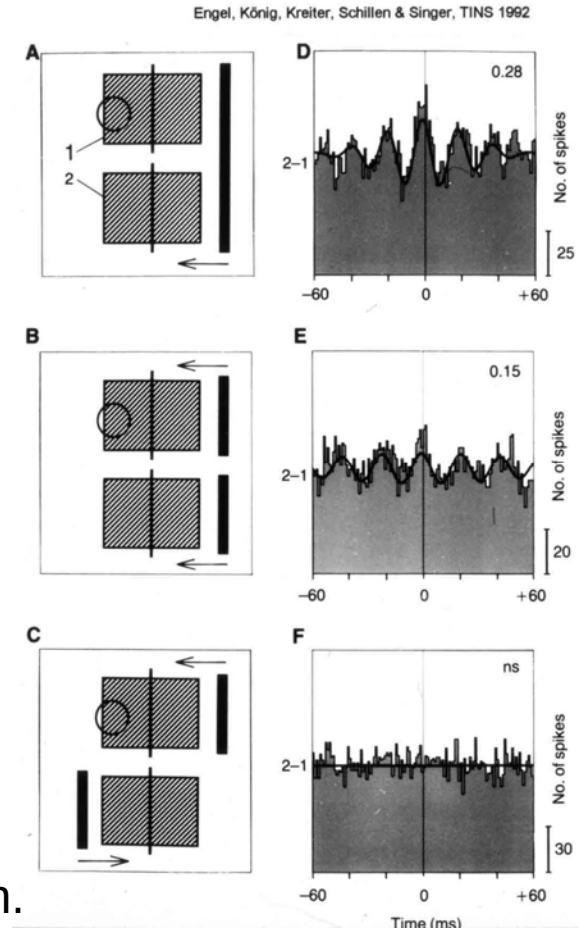
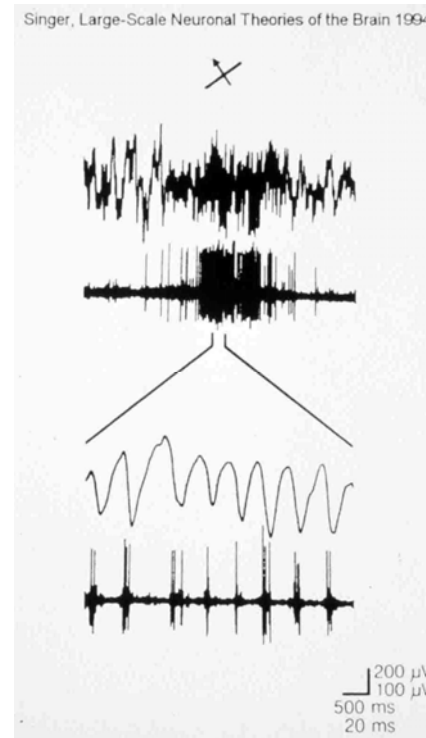
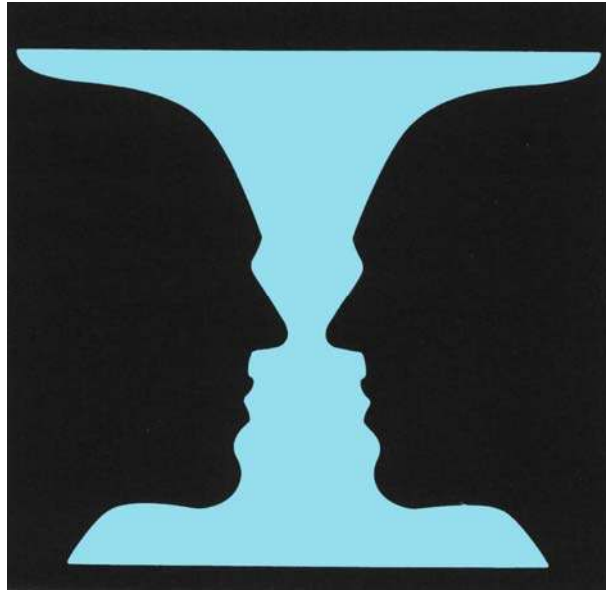
IT cells are selective for complex shapes (e.g. face)

Bilateral lesion of IT results in *prosopagnosia*.

- large receptive fields (+ central area)
- frequent binocular representation

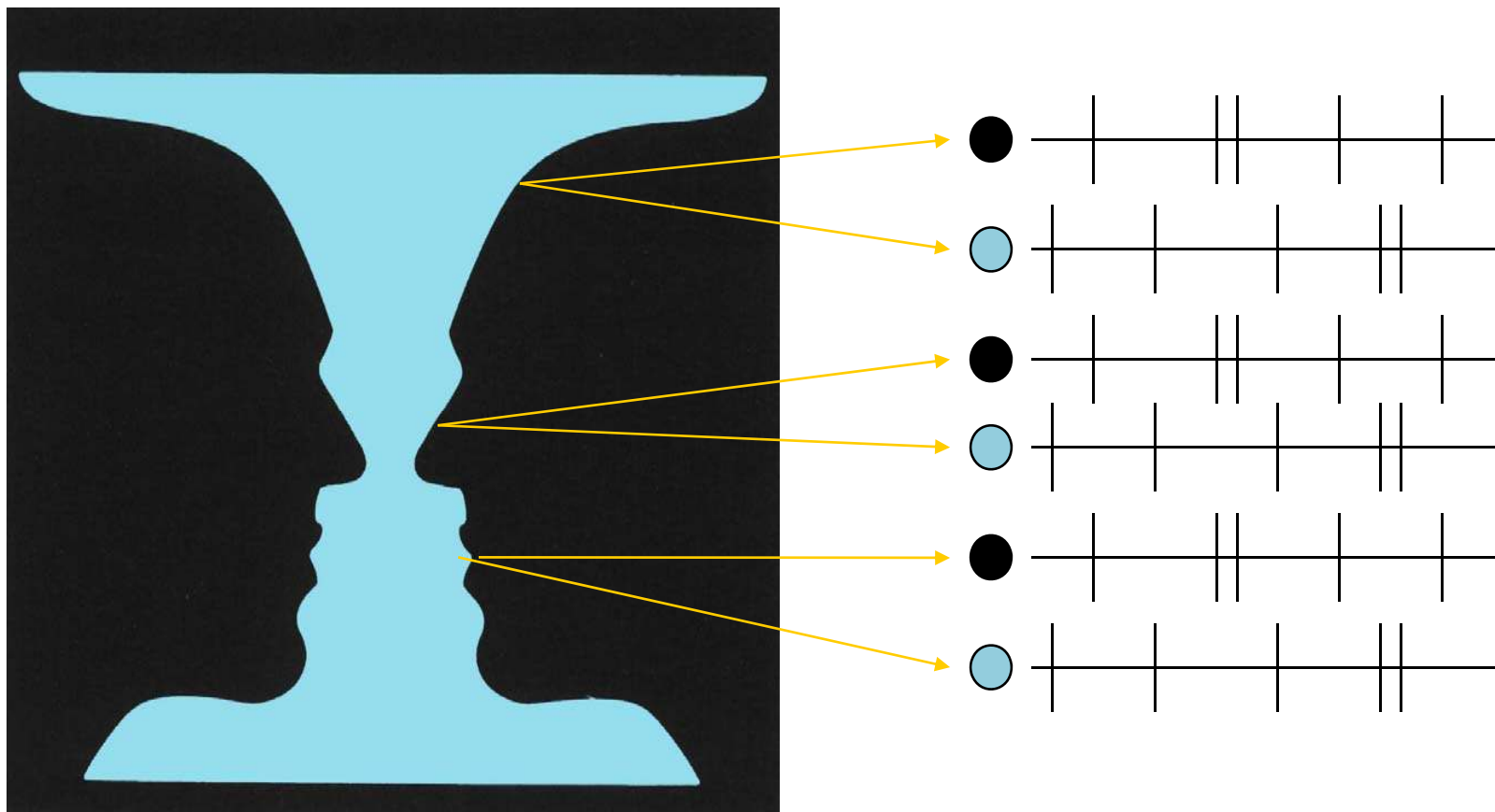


The „binding” problem and its supposed solution



During attention: oscillation and synchronous firing pattern.

Perception is represented by the activity of different neuronal assemblies

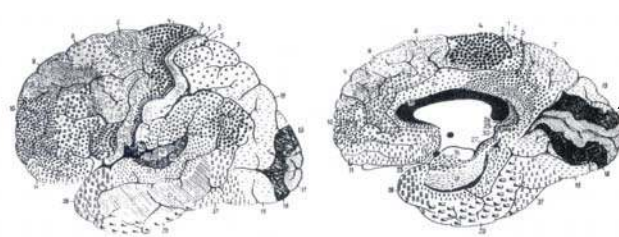


II. Structure and function of the visual cortex.

Pyramidal cell: the basic cell type

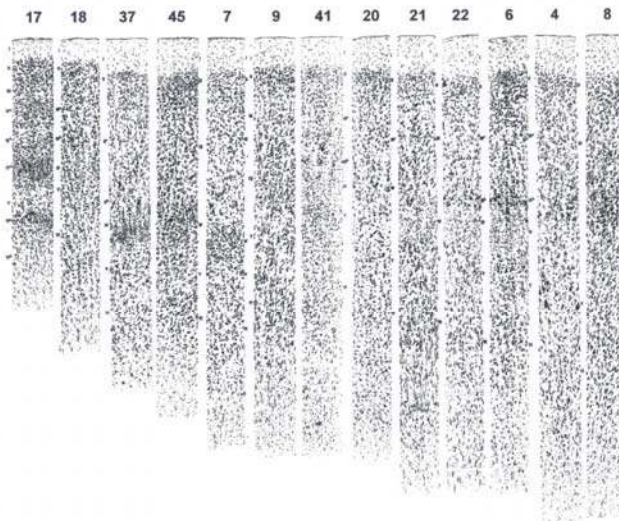


Global architecture of the cerebral cortex



Visual cortex

Nissl-staining (von Economo)



Motor cortex (agranular) Frontal cortex Parietal cortex Occipital cortex (granular) Coniocrortex (granular)

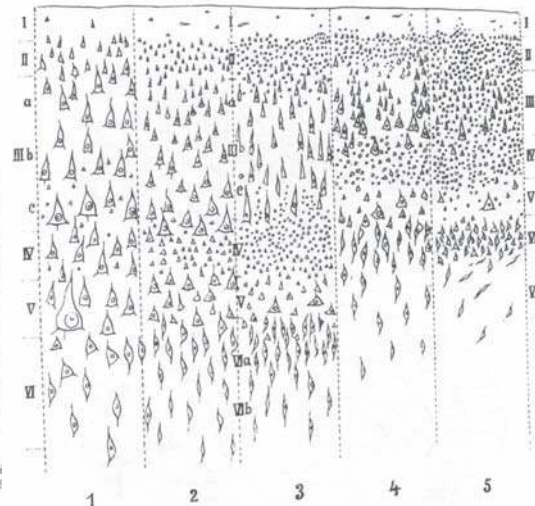


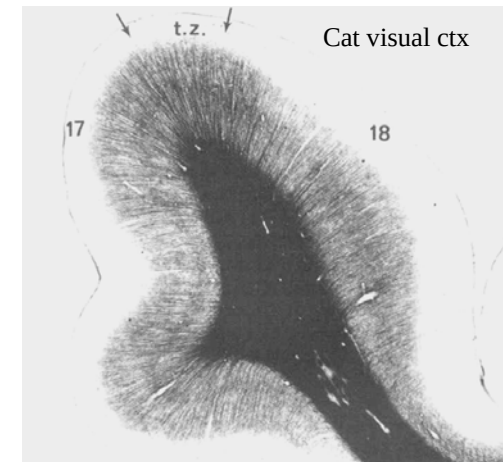
Fig. 9. Diagram showing differences in the cytoarchitecture of different cortical areas in the human brain. Regional variations in cytoarchitecture reflect structural differences in cortical organization fundamental in determining the functional characteristics of cells within. Taken from Brodmann (1905). Translated by Garey (1994). See also Brodmann (1907, 1908), Vogt and Vogt (1919) and Walker (1940).

Table I. Pattern of Lamination in the Striate Area of Man and Various Subhuman Primates According to Various Authors*

Ramón y Cajal (1909–1911)	Brodmann (1909)	von Economo and Koskinas (1925)	Rose (1935)	Bailey and von Bonin (1951)	Garey (1971)	Lund and Boothe (1975)	Braak (1976b)
1	I	I	I	i	I	I	I
2	II	II	II	ii	II	II	II
3	III	III	III	iiia	IIIa	IIIA	IIIA,b
	IVa	(IIIB)	IVa	iiib	IIIB	IVa	IIIC–IVa
4	IVb	(IIIC)	IVba	iva	IIIc	IVB	IVb
			IVbβ			IVCα	IVCα
5		IV	IVc	ivbo	IV	IVCβ	IVcβ
6	IVc						IVd
		Va	Va	ivbβ	V	VA	Va
7	V	Vb	Vb	v		VB	Vb
8	VIa		VI	via			VIa
9	VIb	VI	VII	vib	VI	VI	VIb

* The gray area gives the approximate location of the line of Gennari.

Myelin-staining (Payne, 1990)



Criteria for subdividing visual cortical areas

1. Cytoarchitectural, myeloarchitectural, chemoarchitectural features.
2. Specific connections to other brain regions.
3. Characteristic functional maps.
4. New receptive field characteristics.
5. Special features in processing visual information and in vision-related behaviour.

Nomenclature of visual cortical areas

Subdivisions according to Brodmann: Area 17, 18, 19

Subdivisions in the „new era”:
V1, V2, V3 etc.
MT, IT etc

Classification of cell types in the visual cortex

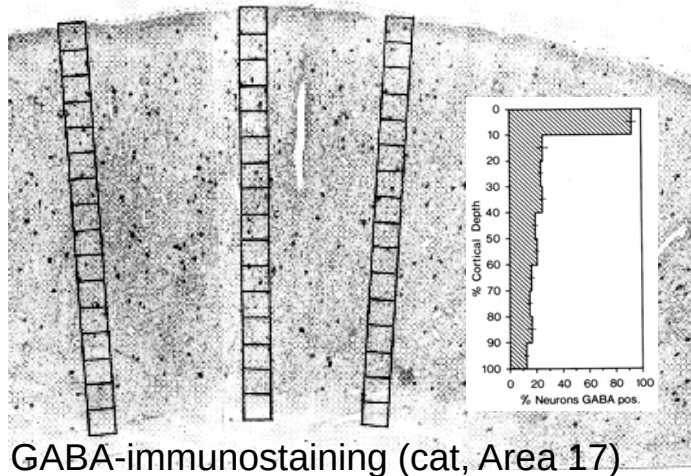
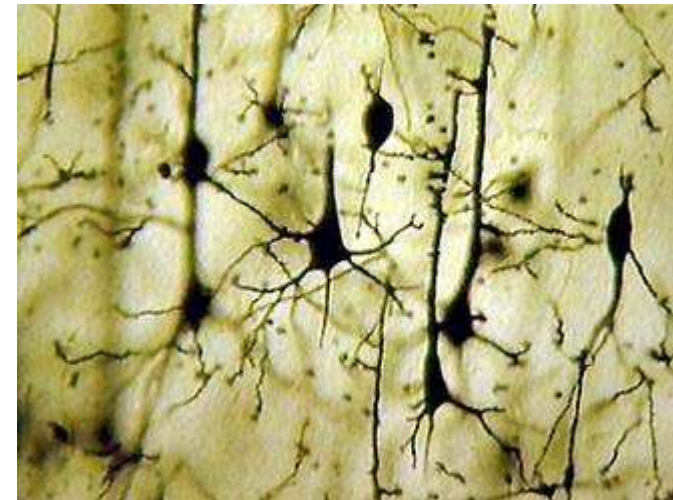
I. Cells with spinous dendrites

- pyramidal cells (2-6 layers)
- spinous stellate cells (4.layer)
- star-pyramidal cells (4. layer)

asymmetric (Gray I.type)synapse
round vesicles in the axon terminal
neurotransmitter: glutamate (Glu)

EXCITATORY

70%

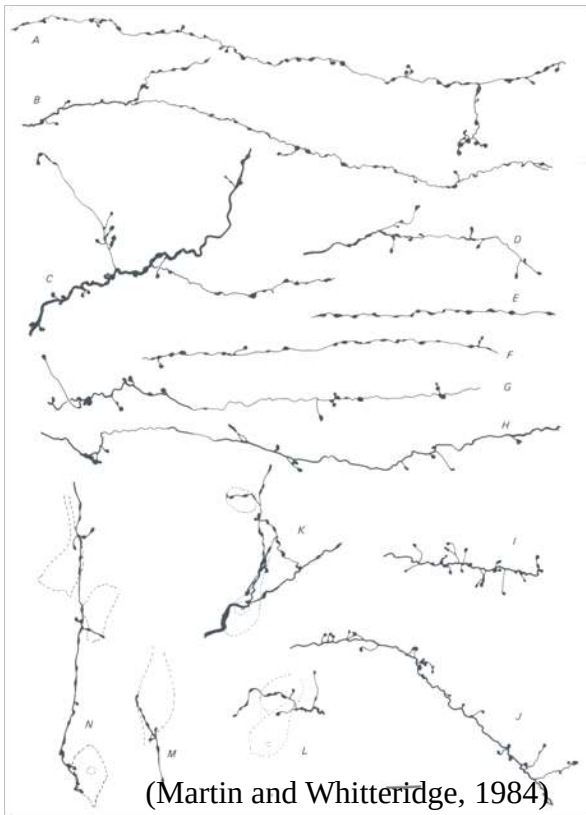


INHIBITORY

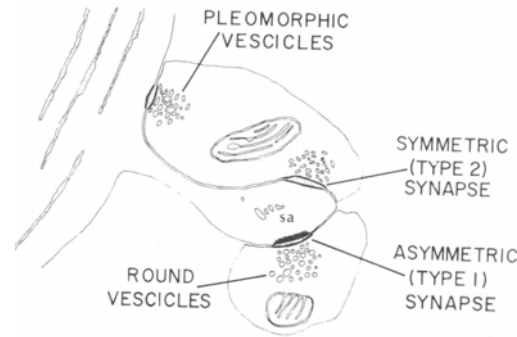
- 20% II. Cells with smooth dendrites (no spines)
diverse morphology (see below)
symmetric (Gray II. type) synapse
pleomorph vesicles in the axon terminals
neurotransmitter: gamma-amino butyric acid (GABA)

Types of axons and synapses in the cerebral cortex

The shape and density of axon terminals are characteristic for the cortical cell type.



(Martin and Whitteridge, 1984)



1-79 - asymmetric
(Gray's type 1)

83-100 - symmetric
(Gray's type 2)

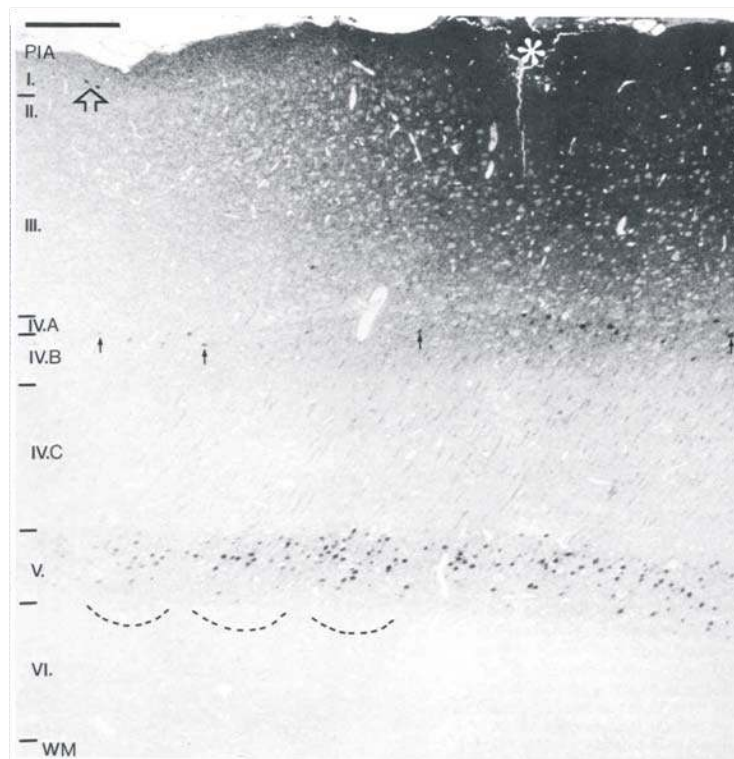
(Colonnier, 1968; Famiglietti, 1970)



Neurotransmitter-specific labelling of pathways

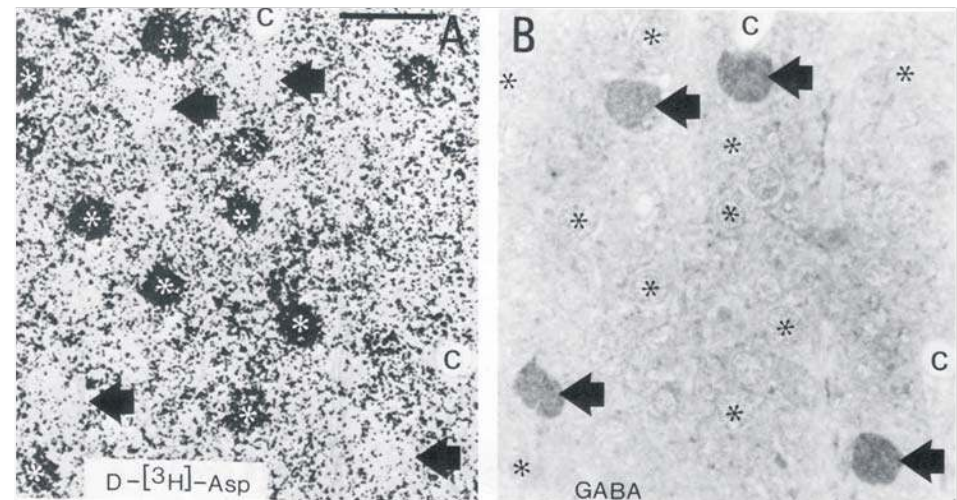
superficial-layers, (2-3) layer

^3H -D-aspartate
(monkey V1, autoradiography)



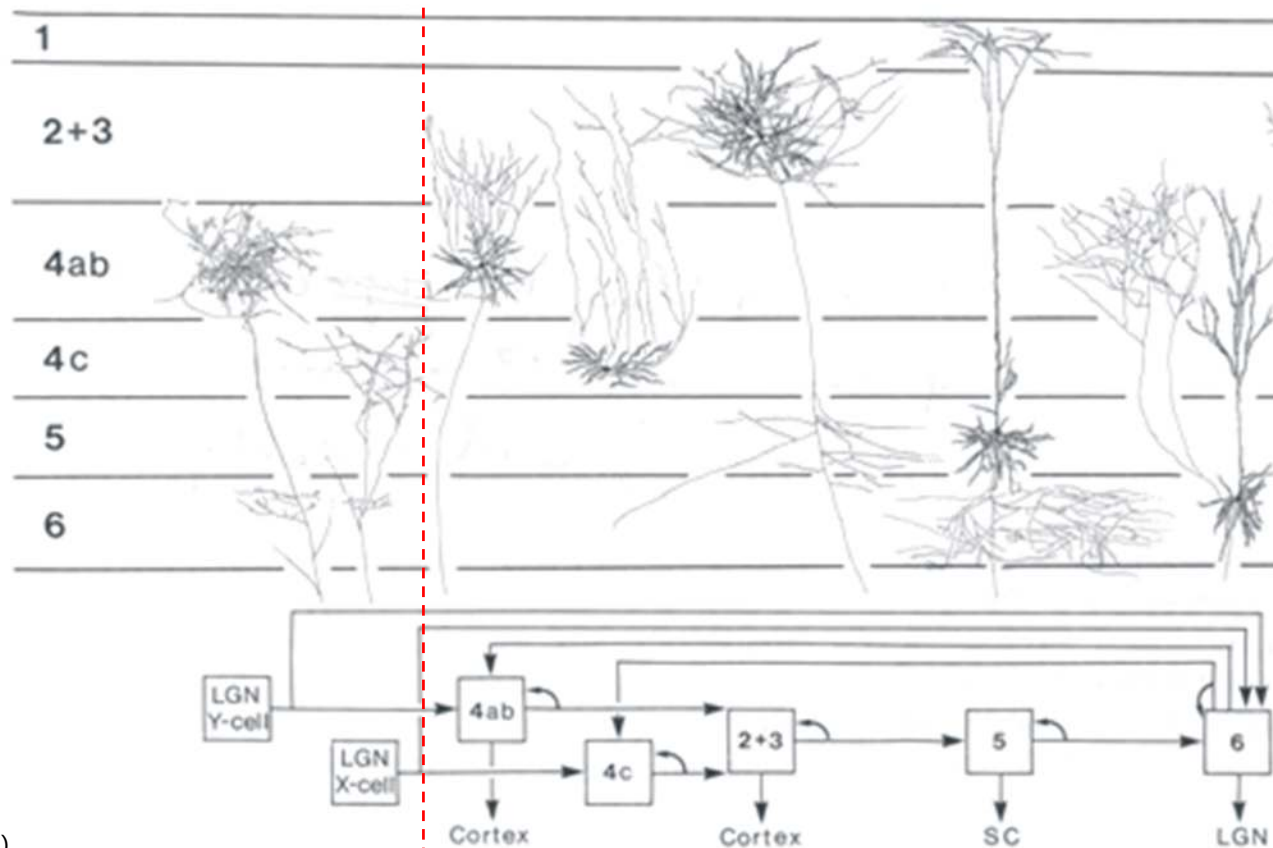
Autoradiography

GABA-immunostaining



(Kisvárdy et al., 1989)

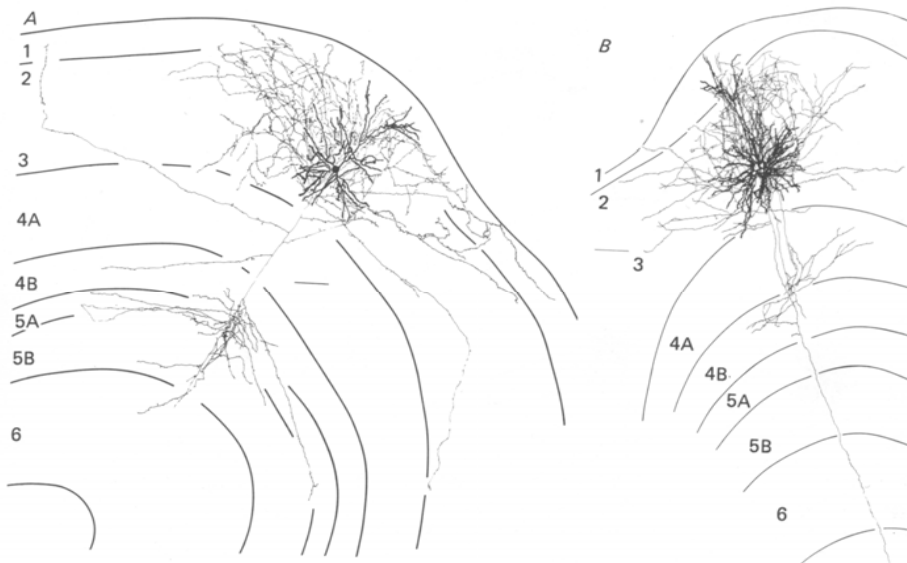
Excitatory intracortical connections in the primary visual cortex – intracellular filling of cells with horse radish peroxidase



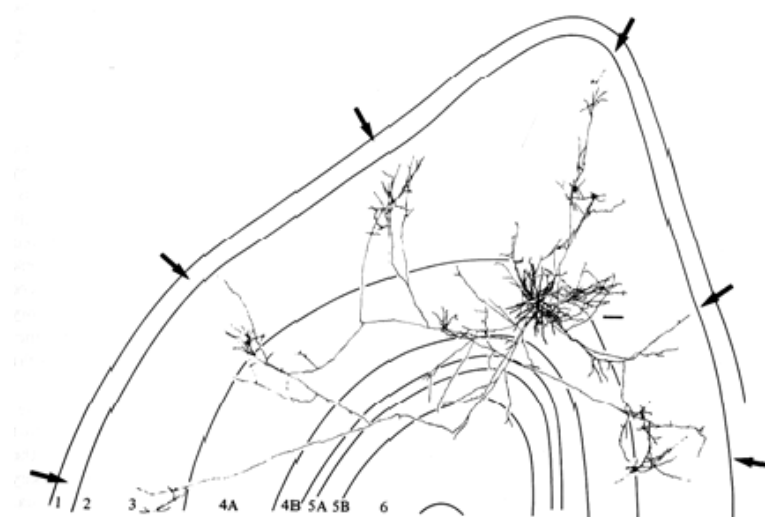
(Gilbert, 1993)

Main types of excitatory neurons (cat, area 17)

Pyramidal cells in the 3rd layer



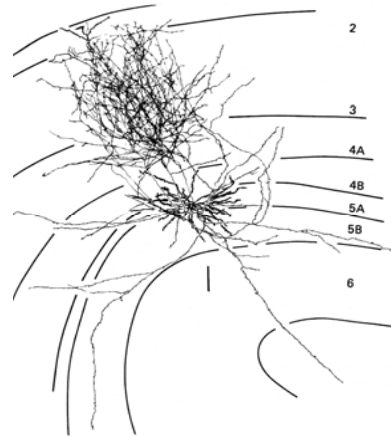
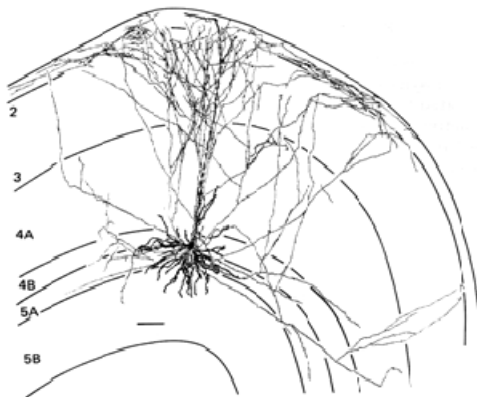
Spinous stellate cell in the 4th layer



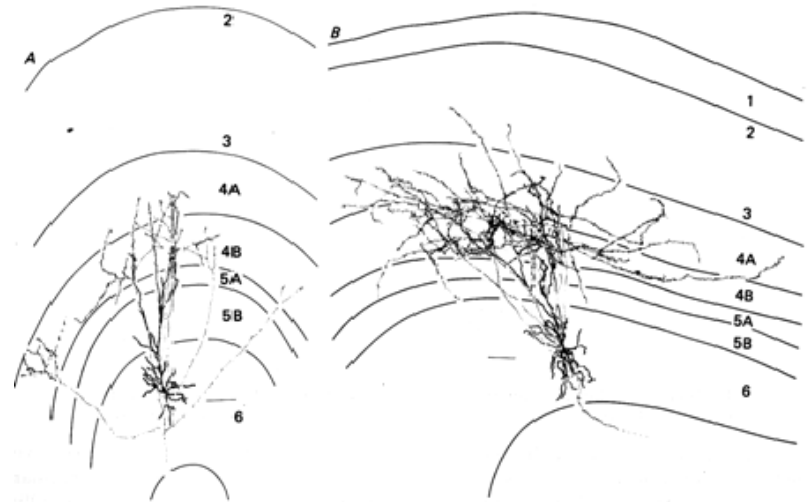
(Martin & Whitteridge, 1984)

Main types of excitatory neurons (cat, area 17)

Pyramidal cells in the 5th layer

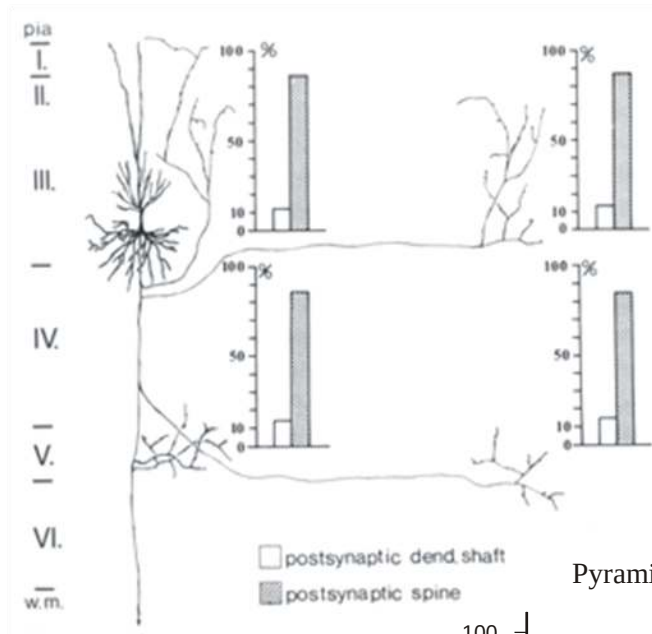
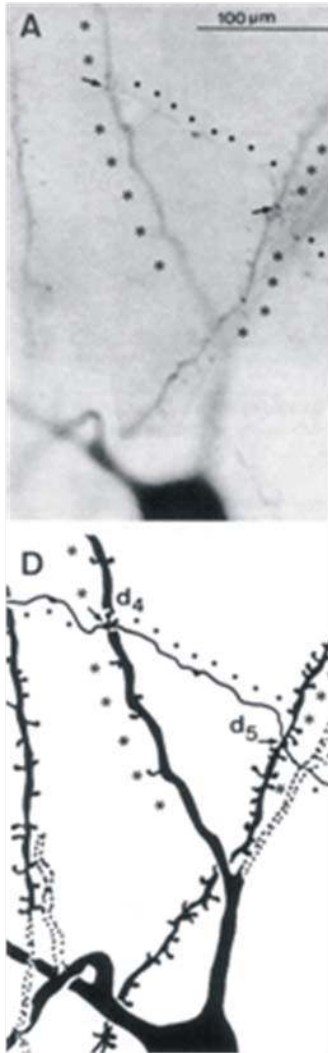


Pyramidal cells in the 6th layer

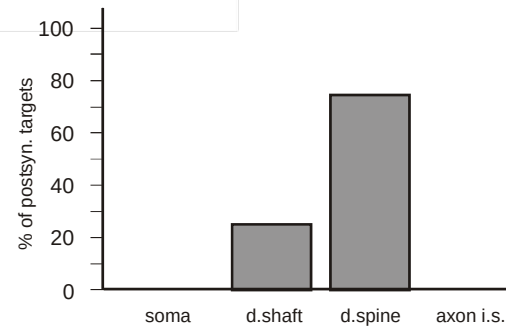


(Martin & Whitteridge, 1984)

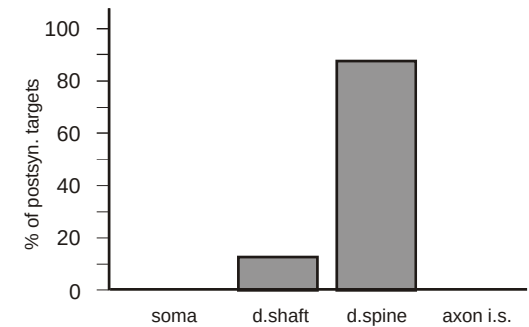
Synaptic targets of the excitatory cells



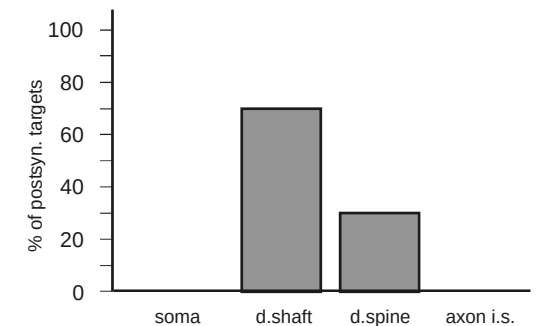
Pyramidal cell in L6



Pyramidal cell in L3

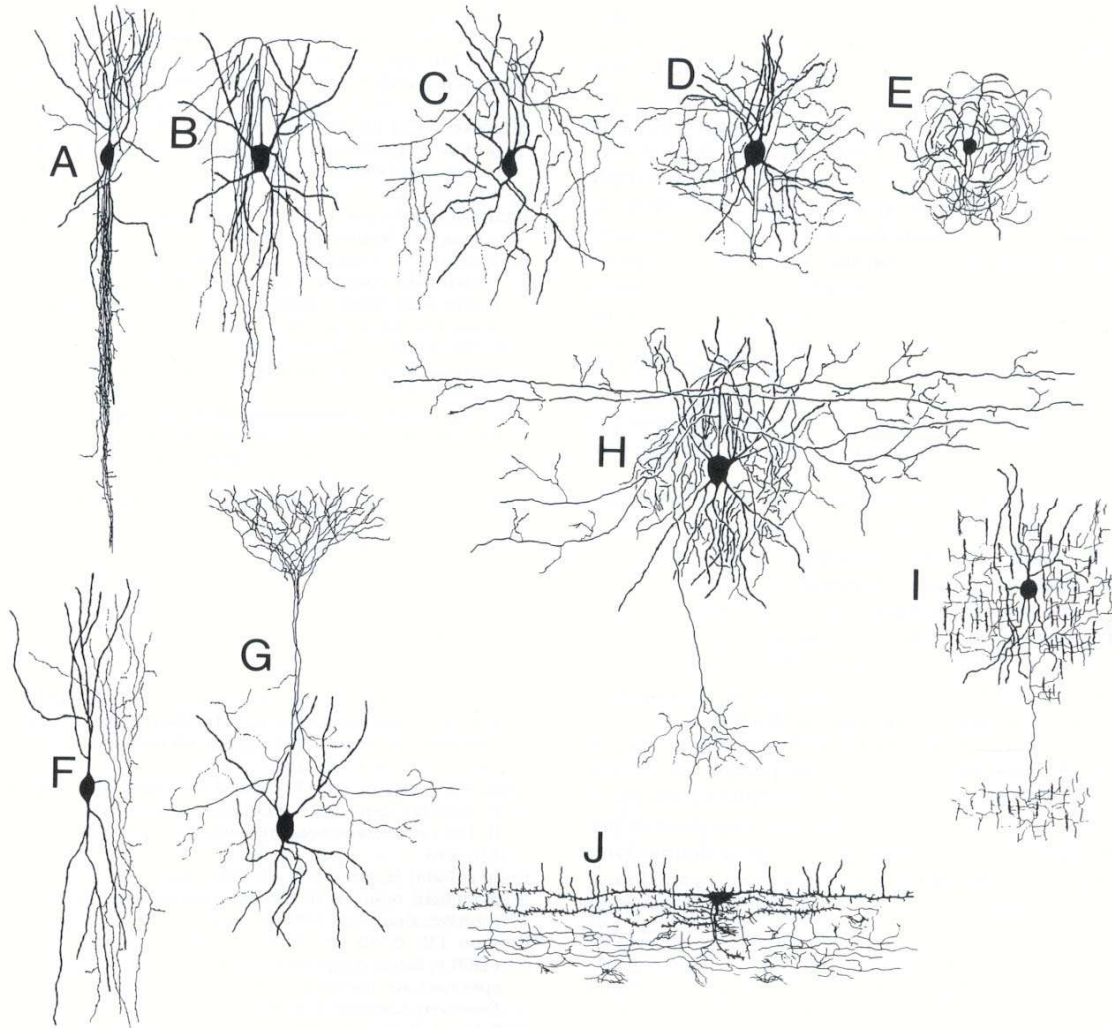


Spinous stellate cell in L4



(Kisvárdy et al., 1986; Ahmed et al., 1994)

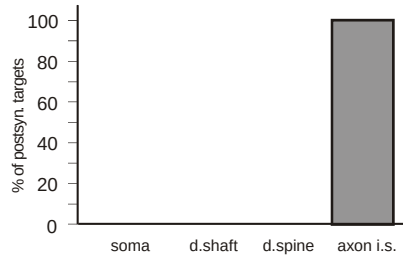
Inhibitory neurons – types of neurons with smooth dendrites or partially spinous dendrites



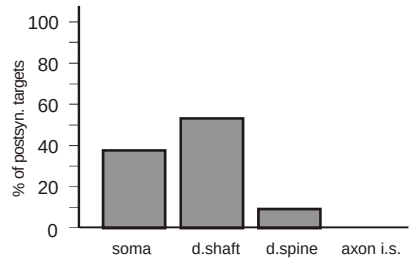
(DeFelipe, 1993)

Distribution of synaptic targets of the various inhibitory neurons

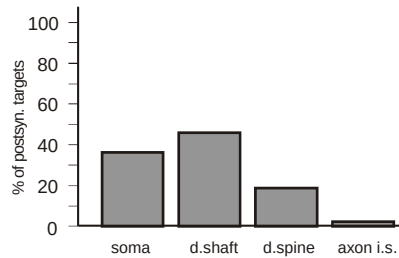
Axo-axonic (chandelier) cell



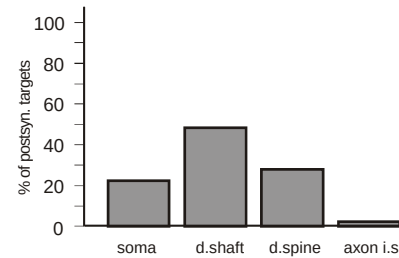
Small basket cell in L2-3



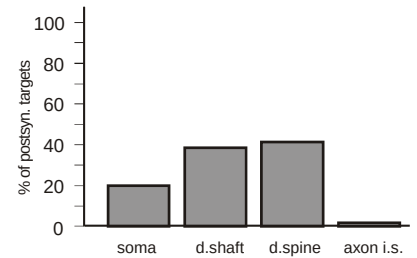
Large basket cell in L3



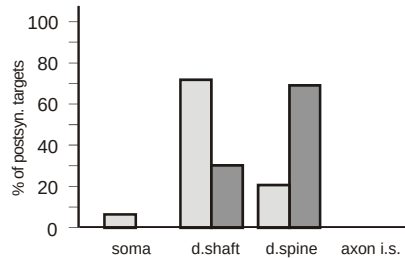
Clutch cell in L4



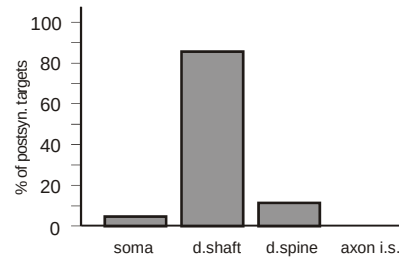
Basket cell in L5



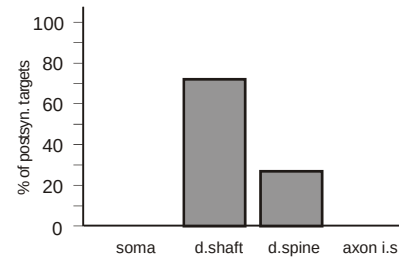
Double bouquet cell



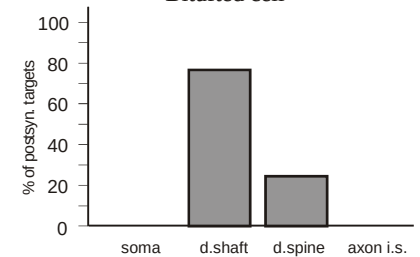
Dendrite-targeting cell



Neurogliaform cell

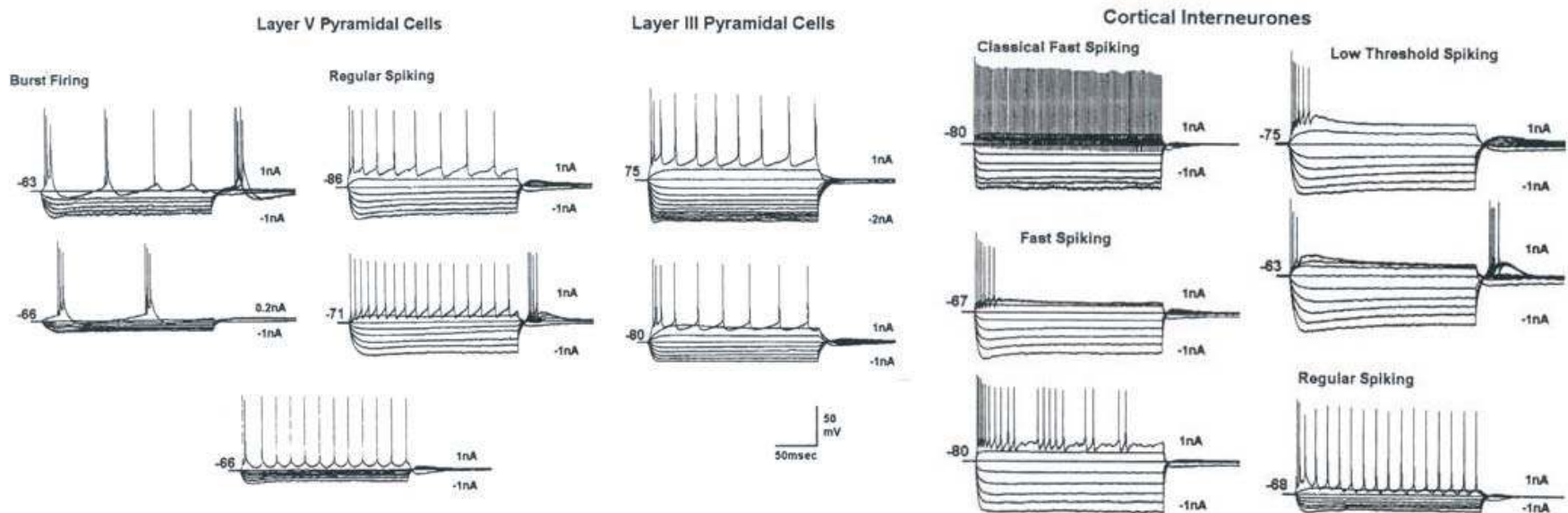


Bitufted cell



Electrophysiological characteristics of the cortical neurons

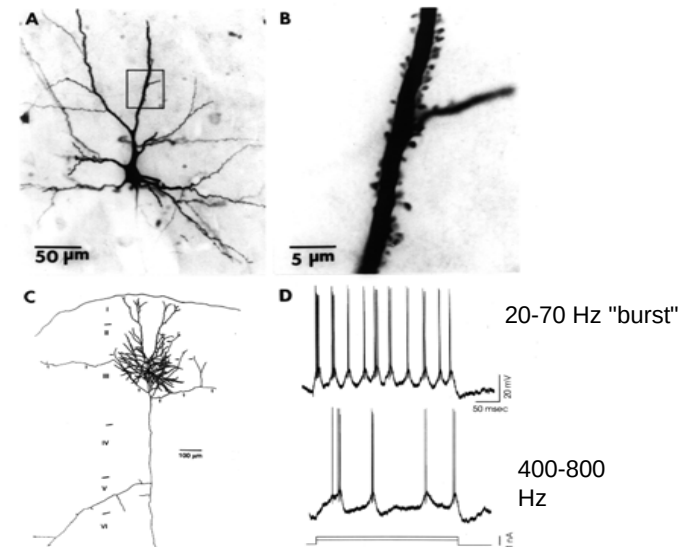
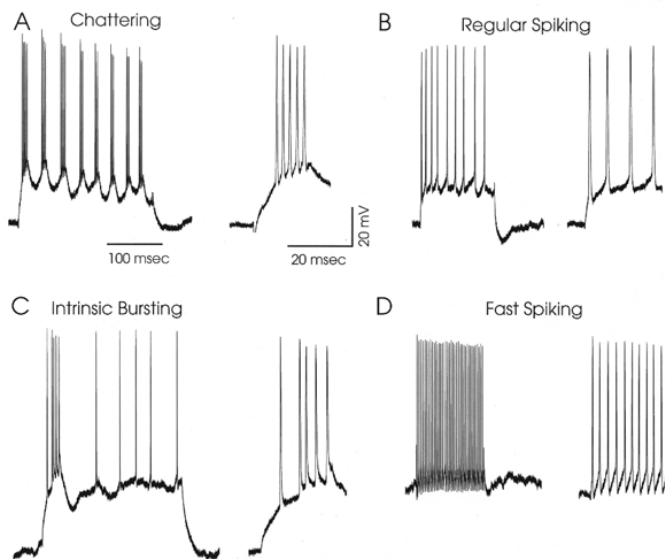
In vitro



(Thomson and Deuchars, 1997)

Electrophysiological characteristics of the cortical neurons

In vivo



(Azouz et al. 1997; Gray and McCormick, 1996)

Colocalization of neurotransmitters, neuropeptides and calcium-binding proteins in neocortical neurons

Table 1

Colocalization of transmitters (or their synthesizing enzymes), neuropeptides, and calcium-binding proteins

	GABA ^a	Cal	Asp	PAG	Calb1	TH
Cal	10% R(4)		17% R(5)	NO	NO	NO
Asp	NO	15% R(5)		NO	NO	NO
PAG	NO	NO	NO		0% R(21)	NO
GABA ^a		11% R(4)	NO	NO	X% R(20) X% R(31)	X% H(48) X% R(25)
Calb1	52% R(28) X% R(31)	NO	NO	0% R(21)		NO
TH	50% H(48) +++ R(25)	NO	NO	NO	NO	
CCd	80-95% M(14) 88% C(3) 100% C(14,45)	NO	NO	0% R(21)	NO	NO
SRII	80-95% M(14) +++ M.C.R(44) 88% C(3) 100% C(14,45) 80-95% R(33)	NO	NO	0% R(21)	NO	NO
NPY	80-95% M(14) 100% C(3,14)	NO	NO	0% R(21)	NO	NO

Colocalization of neurotransmitters, neuropeptides and calcium-binding proteins in neocortical neurons

TE	1% M(20) 100% M(20) 100% R(40)	2-4% C(6)	NO	NO	NO	NO
VIP	0% C(9) X% R(31)	NO	NO	0% R(21)	X% R(12) X% R(31)	NO
CRF	0% C(9)	NO	NO	0% R(21)	NO	NO
PV	100% M(17) 98% M(47) 93% C(11) 100% C(13) ++++ R(1) 100% R(41) 100% R(22)	NO	NO	0% R(21)	NO	NO
CalB	100% M(17) 94% M(47) 30% M(7) 80% C(11) 63% C(9) 100% C(13) 50% R(42) 100% R(22)	NO	NO	0% R(21)	NO	NO
CalR	25% R(42)	NO	NO	NO	NO	NO

For each combination, extent of colocalization, the species, and references are indicated, as follows.

Abbreviations: Asp, aspartate; CalB, calbindin; CalR, calretinin; C, cat; CCK, cholecystokinin octapeptide; ChAT, choline acetyltransferase; CRF, corticotropin-releasing factor; GABA, γ -aminobutyric acid; GAD, glutamic acid decarboxylase; Glu, glutamate; H, human; M, monkey; ms, mouse; ND, not determined; NPY, neuropeptide Y; PAG, phosphate-activated glutaminase; PV, parvalbumin; R, rat; SRF, somatostatin; TH, tyrosine hydroxylase; TK, tachykinin; VIP, vasoactive intestinal polypeptide.

List of subjective terms (which are the most commonly used by the authors to describe colocalization) and corresponding symbols: + + + + +, "with few exceptions," "virtually all," "most, if not all"; + + + +, "the vast majority," "almost all," "the majority"; + + +, "many," "frequently"; + +, "moderate"; +, "little," "few," "very few," "a small portion"; 0%, "no colocalization," "virtual lack of colocalization"; X%, "colocalize" (colocalization with no quantitative or qualitative data).

References: 1, Celio (1986); 2, Celio (1990); 3, Chronwall et al. (1984); 4, Conti et al. (1987a); 5, Conti et al. (1987b); 6, Conti et al. (1992b); 7, DeFelipe and Jones (1992); 8, DeFelipe et al. (1990); 9, Demeulemeester et al. (1988); 10, Demeulemeester et al. (1989); 11, Demeulemeester et al. (1991); 12, Eickstein and Baughman (1984); 13,

Colocalization of neurotransmitters, neuropeptides and calcium-binding proteins in neocortical neurons

Morphological types of chemically identified neurons

Table 4
Morphology of chemically identified neurons

Substance	Pyramidal	Nonpyramidal
Glu, Asp	Most	Few
GABA, GAD		All
ChAT		All
TH		All
CCK, SRIF, NPY, TK, VIP, CRF	Few*	Most
PV		All
CalB	Many	Most
mAb Cat 301	Many	Many
mAb VC1.1, mAb HNK-1, mAb 383, mAb 473, mAb 376		All [†]
VVA, SBA		All [†]

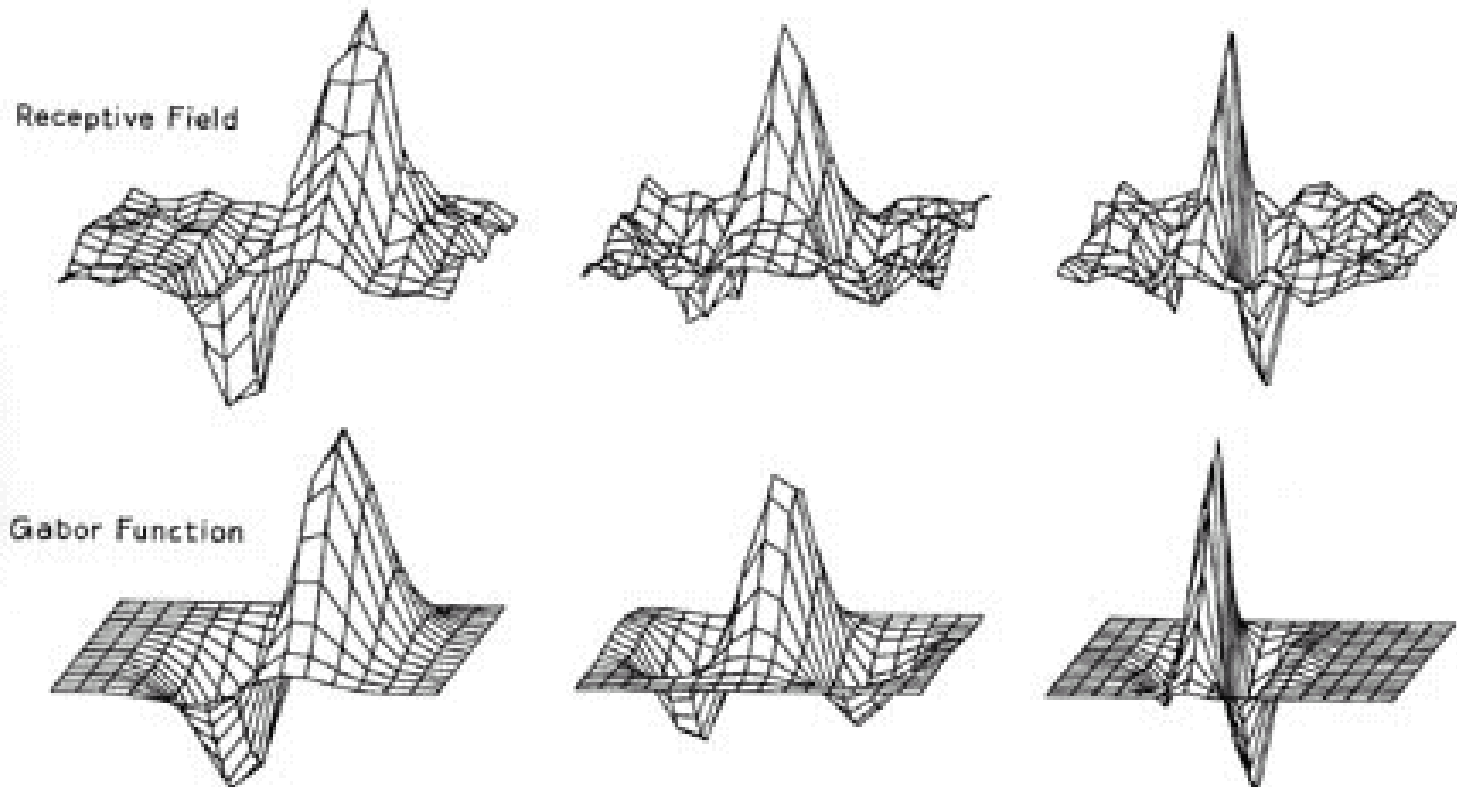
For abbreviations, see Table 1.

* There is some controversy about the existence of peptidergic pyramidal cells (see *Morphology and Chemical Characteristics of Neocortical Cells*).

[†] Occasionally pyramidal cells are stained for mAbs VC1.1 (Naegale et al., 1988), 473, and 376 (Morino-Wannier et al., 1992) and for the lectin VVA (Kosaka and Heizmann, 1989).

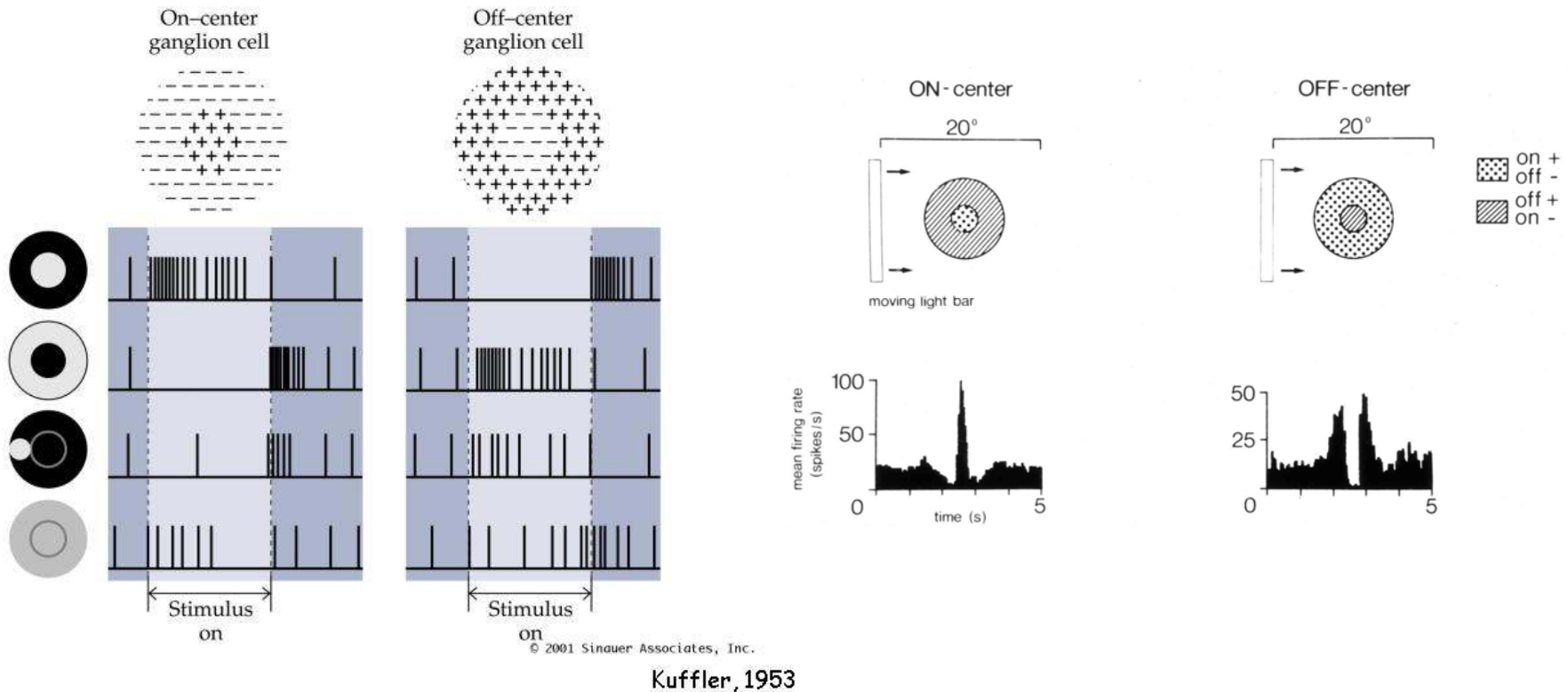
(DeFelipe, 1993)

III. The receptive field. Functional studies on the orientation and direction selectivity.

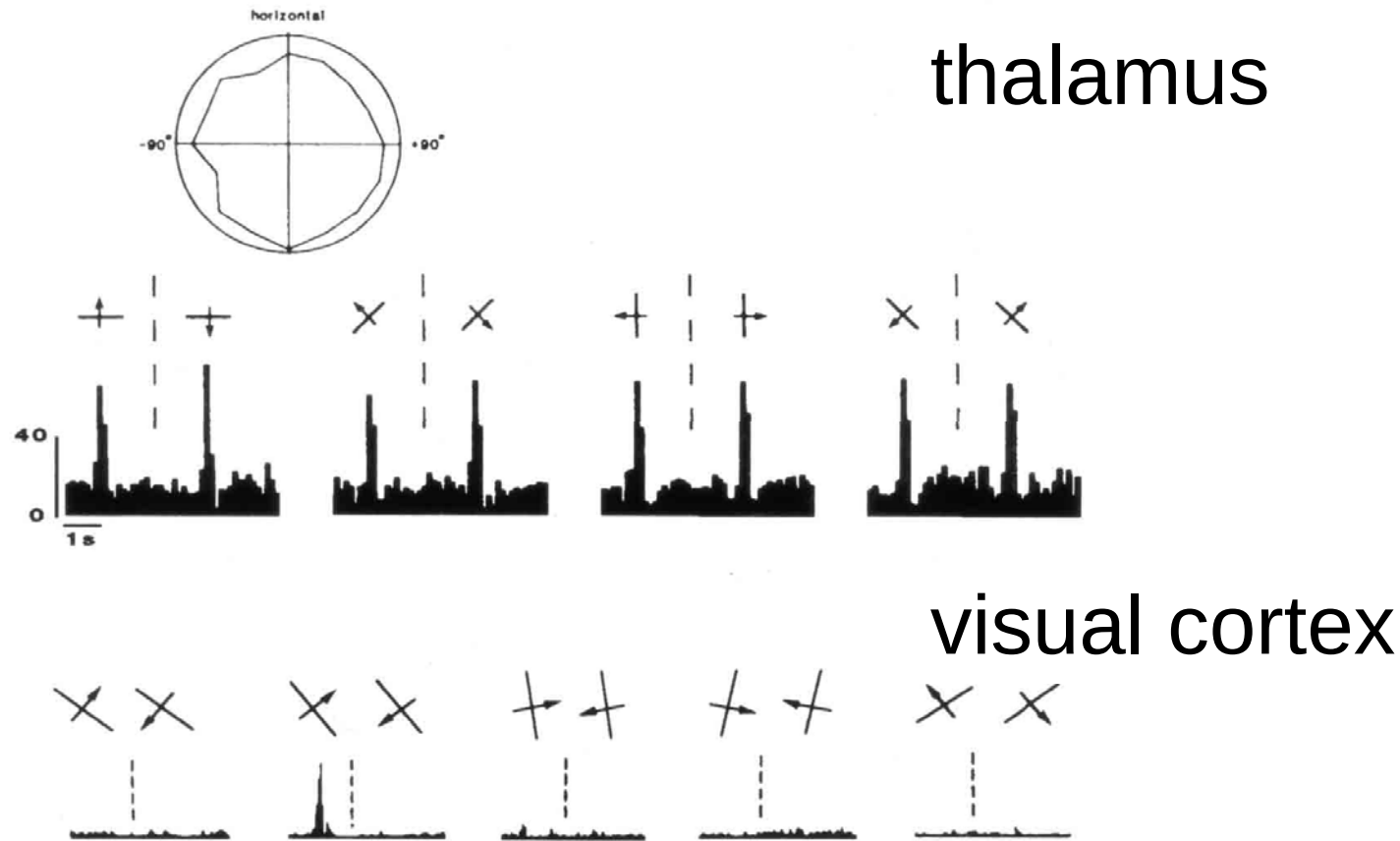


Basic feature of the primary input of the visual cortex: antagonistic „center-surround” structure

Retina and thalamus

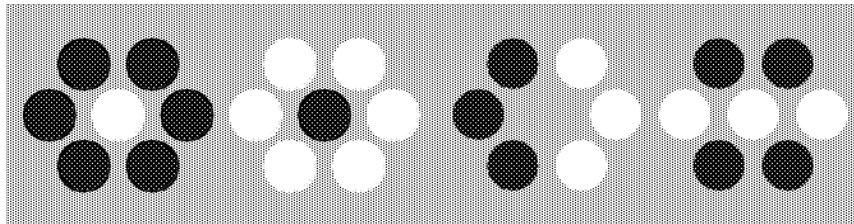


Features of the receptive field show robust changes in the visual cortex

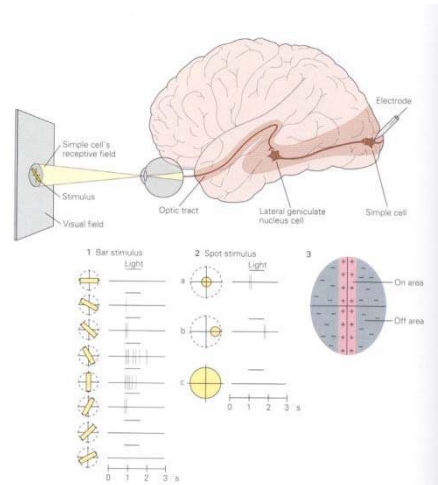


Theory of the formation of „simple”-typed receptive field in the primary visual cortex (Hubel and Wiesel, 1962)

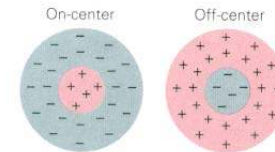
retinal ON retinal OFF cortical simple ODD EVEN



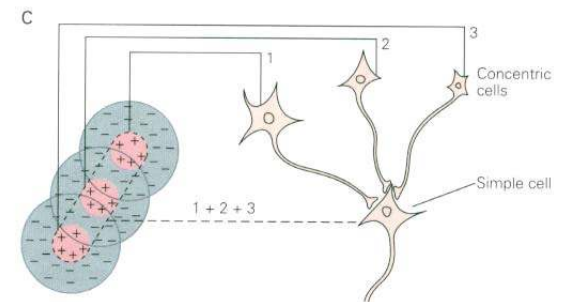
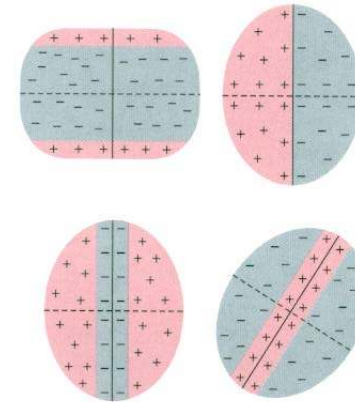
Plotting the receptive field



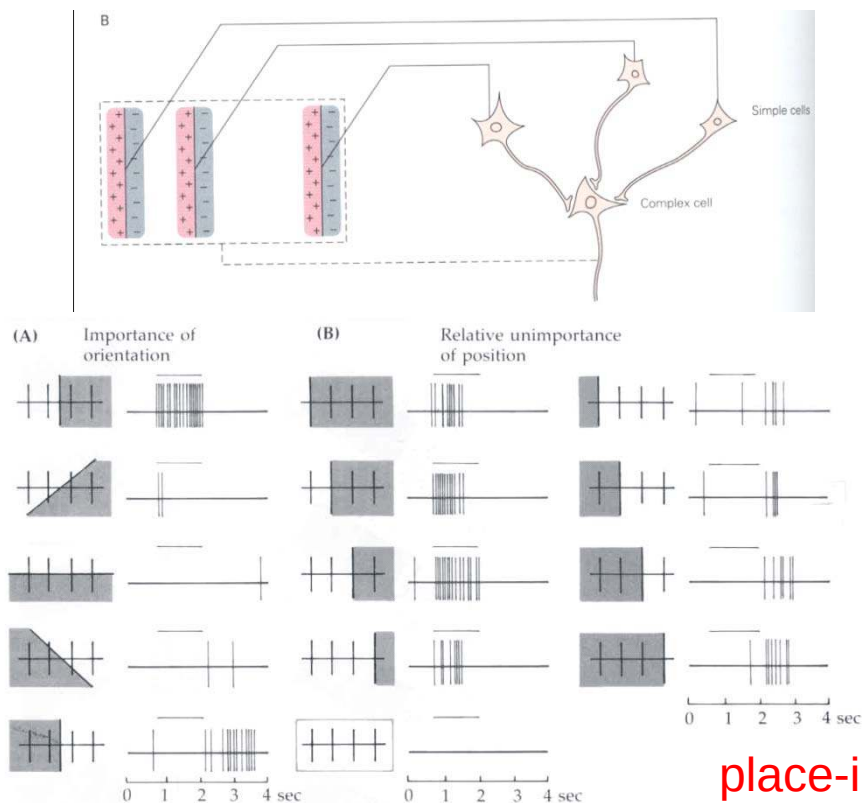
A Receptive fields of concentric cells of retina and lateral geniculate nucleus



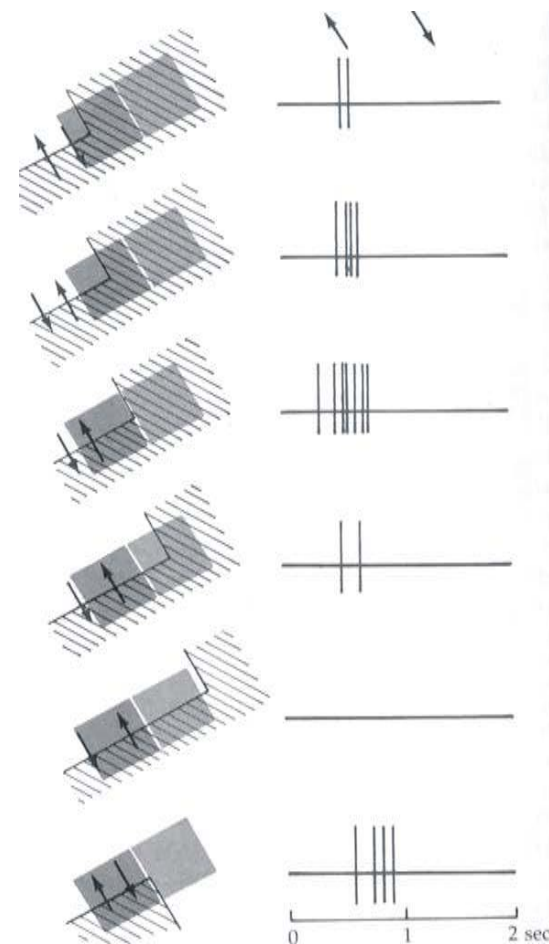
B Receptive fields of simple cells of primary visual cortex



Theory of the formation of „complex”-typed receptive field in the primary visual cortex (Hubel and Wiesel, 1962)



End-inhibition

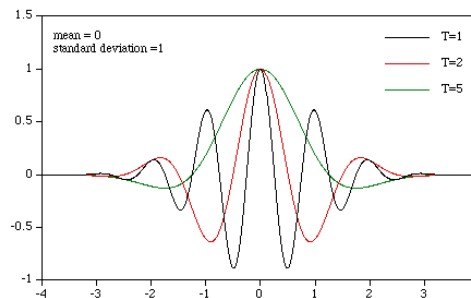


Structure of the receptive field in the visual cortex can be modelled with the aid of „Gabor function”

Daugman J, 1940

1-dimensional "Gabor-function"

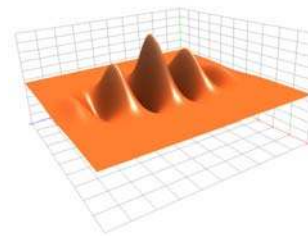
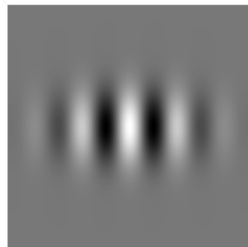
$$\text{gabor}(x) = \exp(-0.5 (x-m)^2 / s^2) \cos(2 \pi (x-m) / T)$$



T= number of cos cycles under the area
s=SD
m=centrum

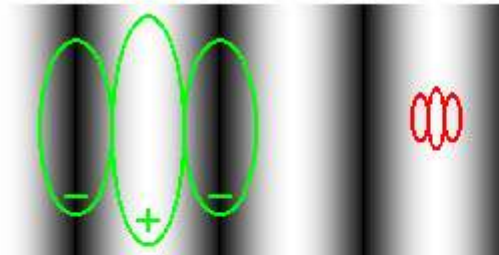
2-dimensional "Gabor-function"

$$\text{gabor}(x,y) = \exp[-0.5 (x-m_x)^2 / s_x^2] \exp[-0.5 (y-m_y)^2 / s_y^2] \cos(2 \pi (x-m_x) / T)$$



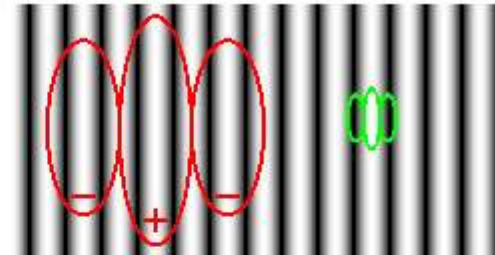
Simple cell receptive fields

Simple Cell Receptive Fields (SC=Simple Cell, RF=Receptive Field)



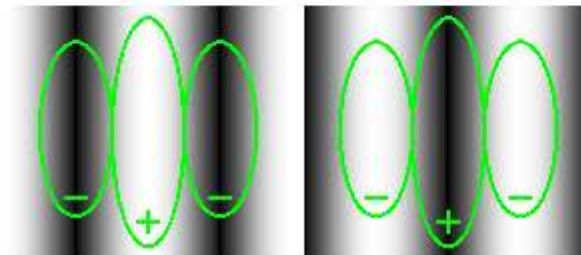
SPATIAL FREQUENCY:

The SC with the RF on the left is tuned to the spatial frequency of this grating. The RF of the SC on the right is too small to pick up this low spatial frequency.



SPATIAL FREQUENCY:

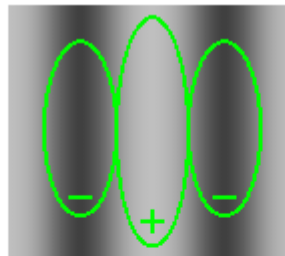
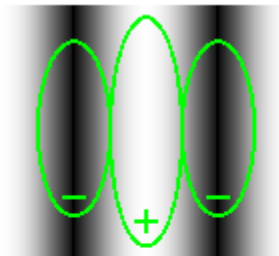
The SC with the RF on the right is tuned to the spatial frequency of this grating. The RF of the SC on the left is too large to pick up this high spatial frequency.



PHASE:

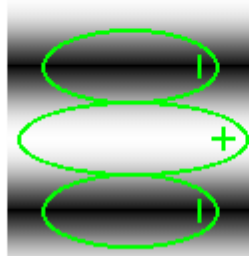
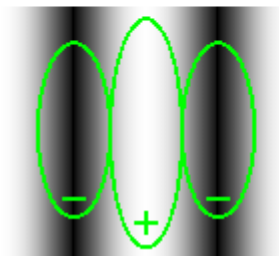
The phases of the two gratings at left differ with respect to the RFs. The SC with the RF at the far left will be excited, while the SC with the RF at the near right will be inhibited.

Simple cell receptive fields



CONTRAST:

The contrasts of the two gratings at left differ. The SC with the RF at the far left will be more excited than the SC with the RF at the near right.



ORIENTATION:

The SCs with the RFs at left are tuned to different orientations because of the difference in spatial orientation of the two RFs.

Mechanism of formation of orientation selectivity I.

"Feed-forward" model

Prediction (based on the H&W model):

- the stronger the orientation selectivity ("RF aspect ratio")
the greater the difference will be between responses evoked by the optimal
and null-orientation
- small deflection from the optimal orientation → large portion of the stimulus
falls out of the receptive field

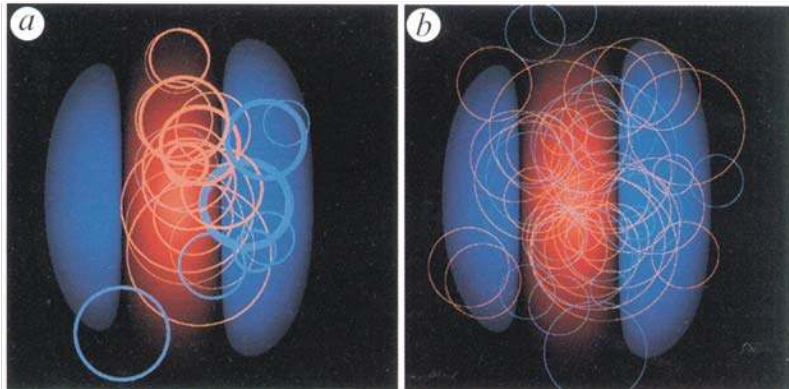
The greater the "aspect ratio" is the more selective the cell!

Mechanism of formation of orientation selectivity I.

Spatial relation of the receptive fields of cortical „simple“ cells and thalamic cells

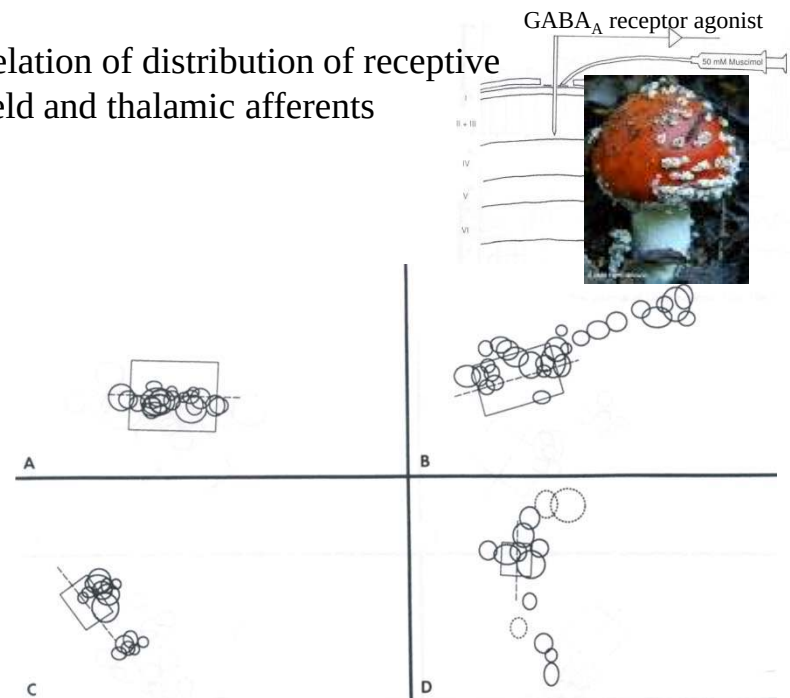
Bound (n=23)

Unbound (n=51)



(Reid and Alonso, 1995)

Relation of distribution of receptive field and thalamic afferents



(Chapman et al., 1991)

Contrast invariance

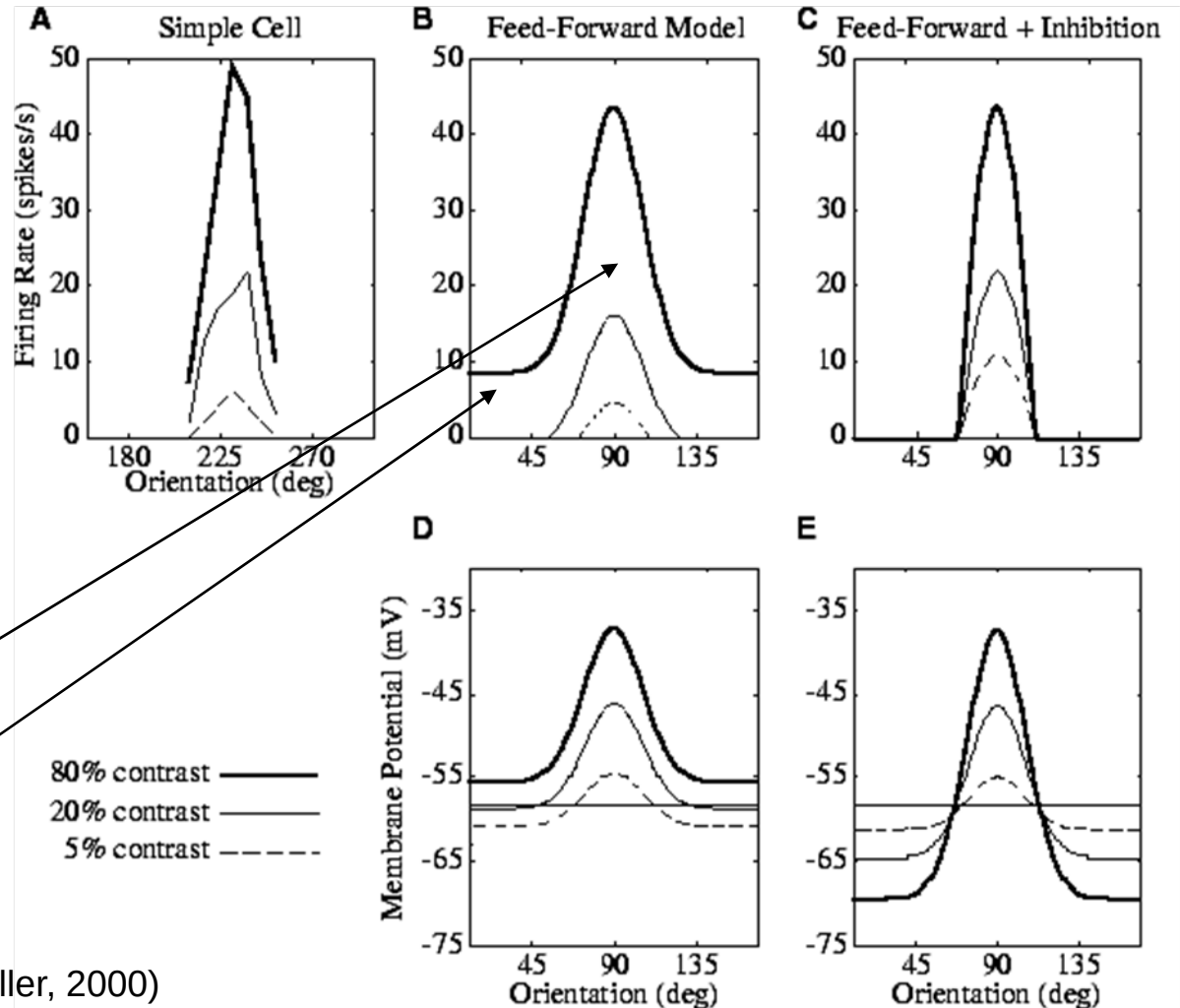
Firing intensity of thalamic cells changes parallel with the extent of contrast (100 i/s).

Consequence: the response is intensifying with non optimal orientation
with increasing contrast the response of "simple" cell is intensifying

Why? Spontaneous activity thalamic cells: 10-15 i/s
1. OFF center thalamic input is saturating (zero i/s)
2. ON center input evokes intensifying **netto** response

Model prediction: Response given at high contrast to non optimal orientation can be stronger than the response given at low contrast to optimal orientation („ice-berg“ effect).

Contrast invariance



"Ice-berg" effect

"spike-threshold"

(Ferster and Miller, 2000)

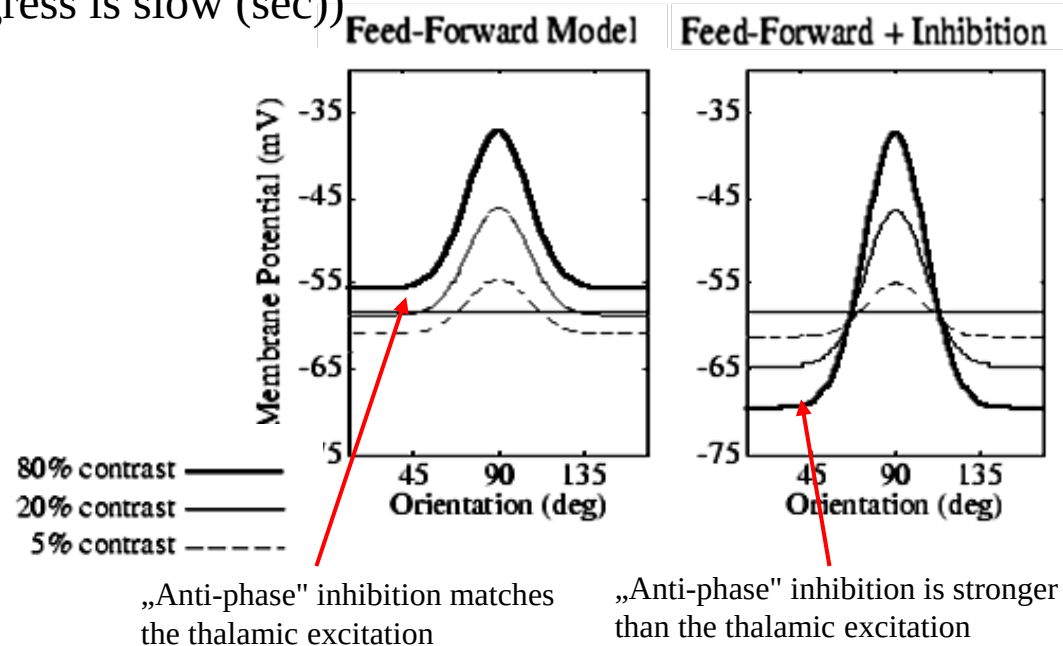
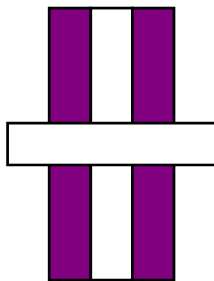
Potential mechanisms of triggering „spike-threshold” changes

1. The „spike-threshold” is independent of contrast – it can be demonstrated intracellularly
2. Frequency dependent depression of thalamic synapses - it does not play significant role (it is too slow and not sufficiently strong)
3. Contrast dependent hyperpolarization (contrast adaptation) – it is unlikely (it is absent by non-optimal orientation, its progress is slow (sec))

4. Inhibition – push-pull inhibition or „anti-phase” inhibition

"ANTI-PHASE" INHIBITION IS STRONGER THAN THE EXCITATION

OFF ON OFF



Anti-phase inhibition is **2-5-fold stronger**,
than the thalamic excitation

Neuronal network:

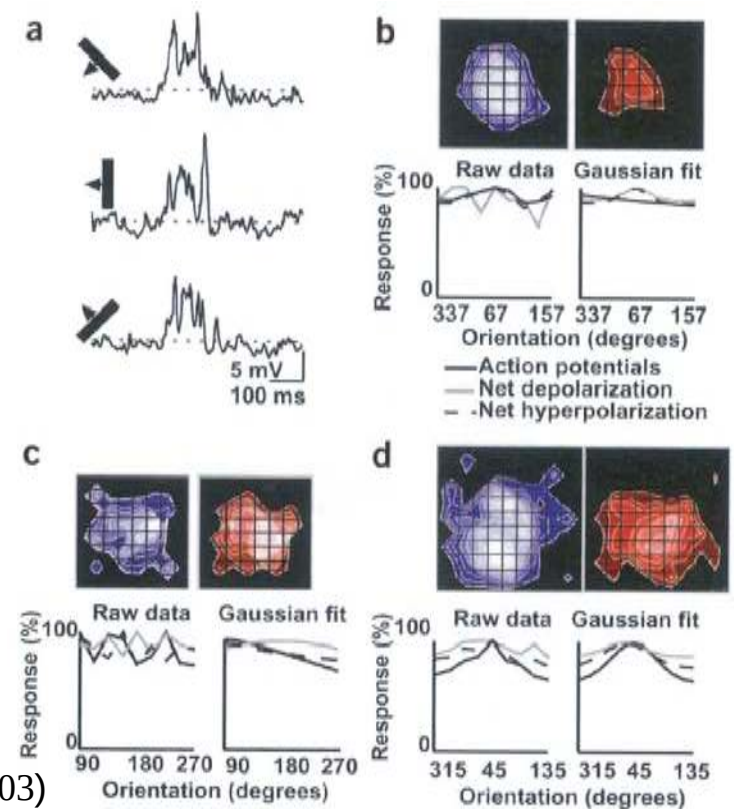
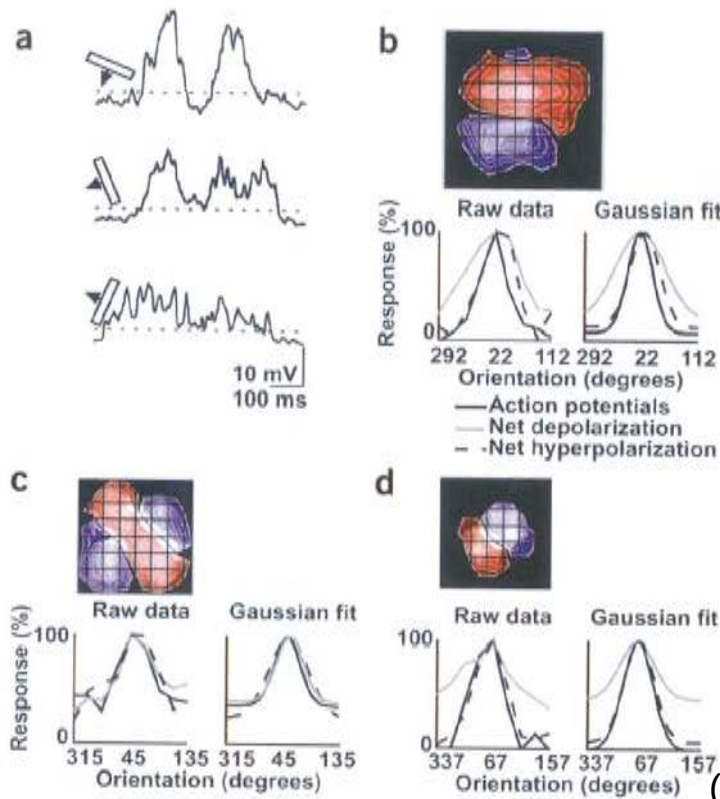
1. Inhibitory thalamic input (DOESN'T EXIST!!)
2. Convergence of many inhibitory cells - all orientations are represented ("push-pull" arrangement)
3. Convergence of contrast dependent inhibitory cells - representation of identical orientation ("push-pull" arrangement)

(Troyer et al., 1998)

Inhibitory cells (basket cells) in layer 4

“Simple”-type

“Complex”-type



(Hirsch et al., 2003)

Other features of responses, which must fit in the orientation model

Phenomena:

- 1.) Dependent on the stimulus, the response of "simple" cells is saturating with increasing contrast (suboptimal contrast and spatial frequency saturate faster).
- 2.) Temporal progress of the response given to a stimulus is changing with increasing contrast (phase shift).
- 3.) The temporal frequency tuning is changing with contrast (with increasing contrast, the rise of the response is stronger in the higher temporal frequency range).
- 4.) Superposition of two stimuli results in smaller response than their algebraic sum, even if either of those means zero activity e.g. cross-orientation.

Other features of responses, which must fit in the orientation model

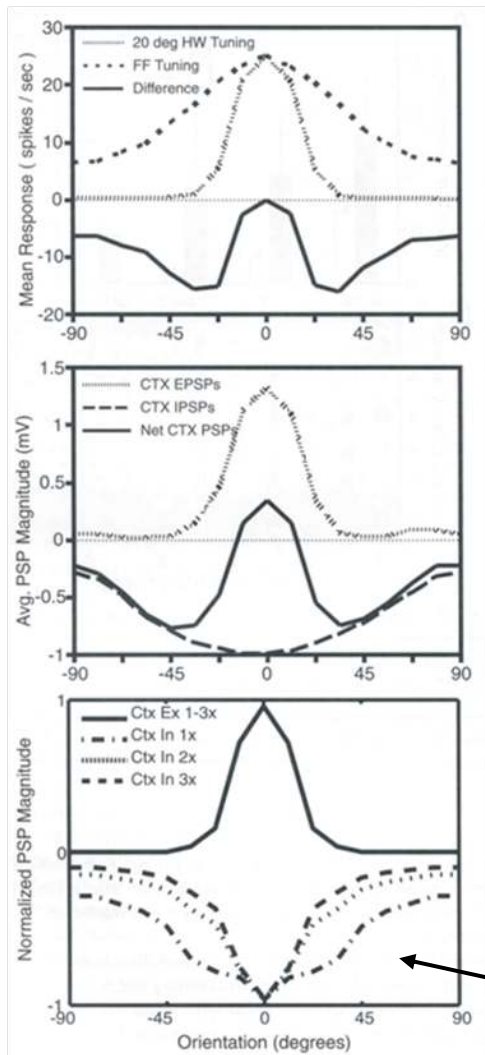
Normalization models:

$$\text{normalised response} = \frac{\text{non-normalised response}}{\text{non-normalised response of all responses}}$$

- normalisation of thalamic input by cortical inhibition
 - result: sigmoid, saturation contrast-function
- (this type of inhibition contains all forms of orientation, thus it is independent of orientation, „pooled”)

Mechanism of formation of orientation selectivity II.

"Feed-back" model



Basic features:

- weak thalamic input
- the thalamic input is not or weakly oriented („aspect ratio“).
- crucial point: orientation selectivity is the result of intracortical excitation and inhibition

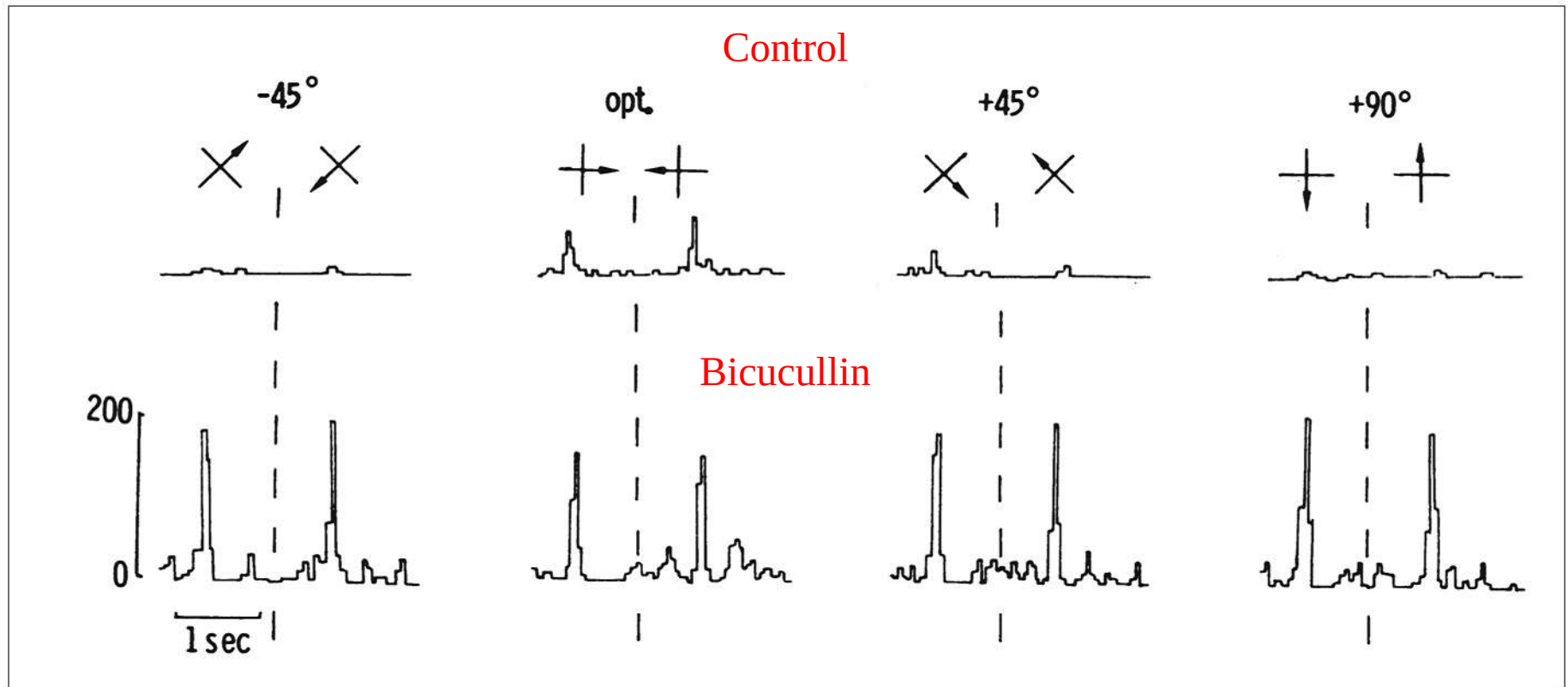
(Somers et al., 1995)

Other features:

- suprathreshold thalamic inputs are enhanced by reverberation mechanisms
- the spatial pattern of the response is determined by the genuine network of the cortex
- the activated cortical pattern is independent of the contrast of the stimulus
- orientation selectivity can be much sharper than the arrangement of the thalamic afferents (greater "aspect ratio")

The stronger is the cortical excitation compared to the thalamic excitation, the narrower the orientation tuning of the necessary inhibition will be.

The intracortical inhibition sharpens the orientation selectivity



(Sillito, 1975)

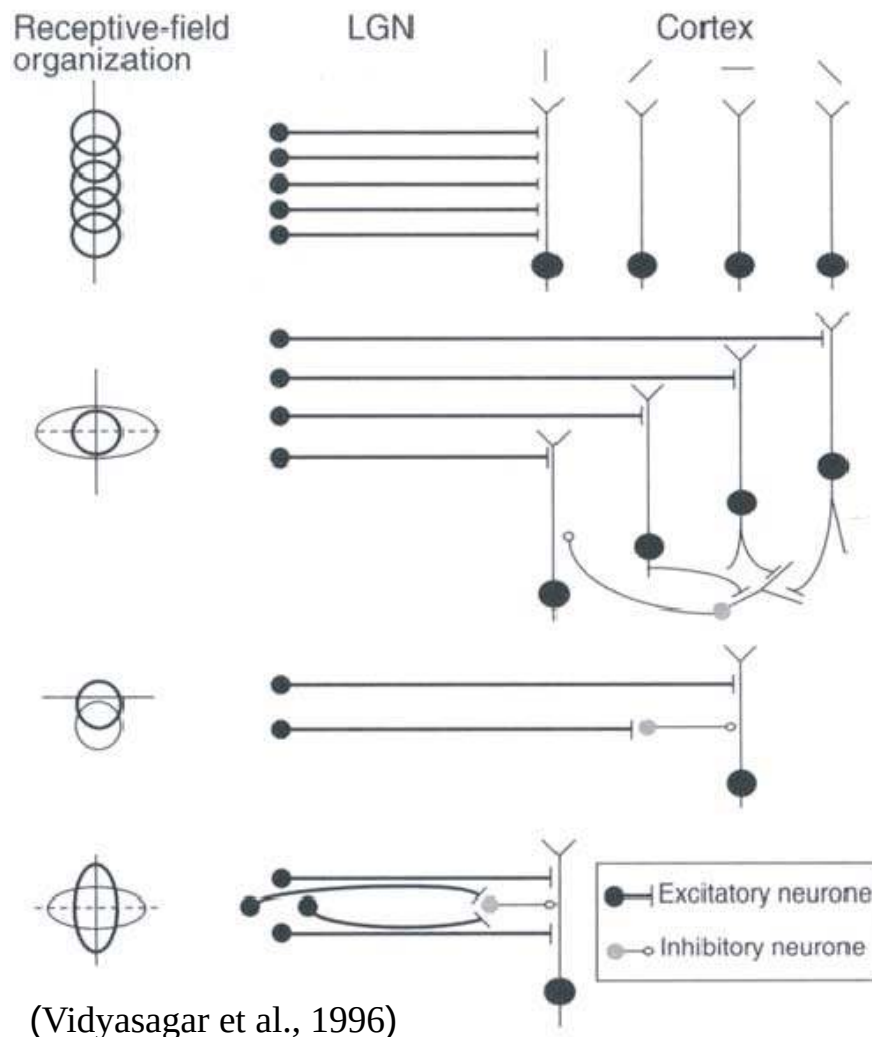
Alternative models for the formation of orientation selectivity

Feed-forward convergence

Feed-back cross-orientation inhibition

Partial spatial overlapping of excitatory and inhibitory inputs ("offset")

"Biased" thalamic input



(Vidyasagar et al., 1996)

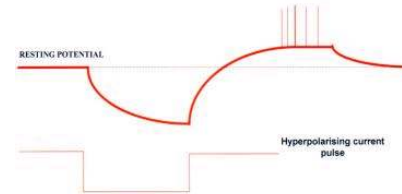
Mechanism of formation of direction selectivity (DS)

Direction selectivity is a contrast invariant feature:
DS is the same for low contrast or high contrast lines.



This contradicts Hubel and Wiesel's (1962) "simple" cell model.

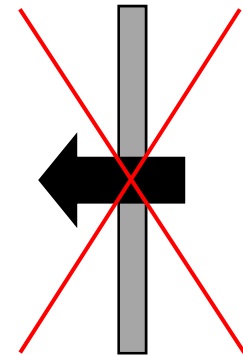
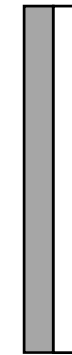
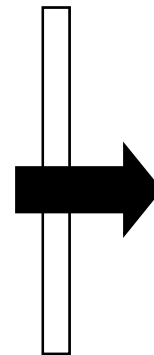
POST-INHIBITORY REBOUND EXCITATION IS A
CLASSICAL NEURAL RESPONSE TO INHIBITION



stimulus

RF

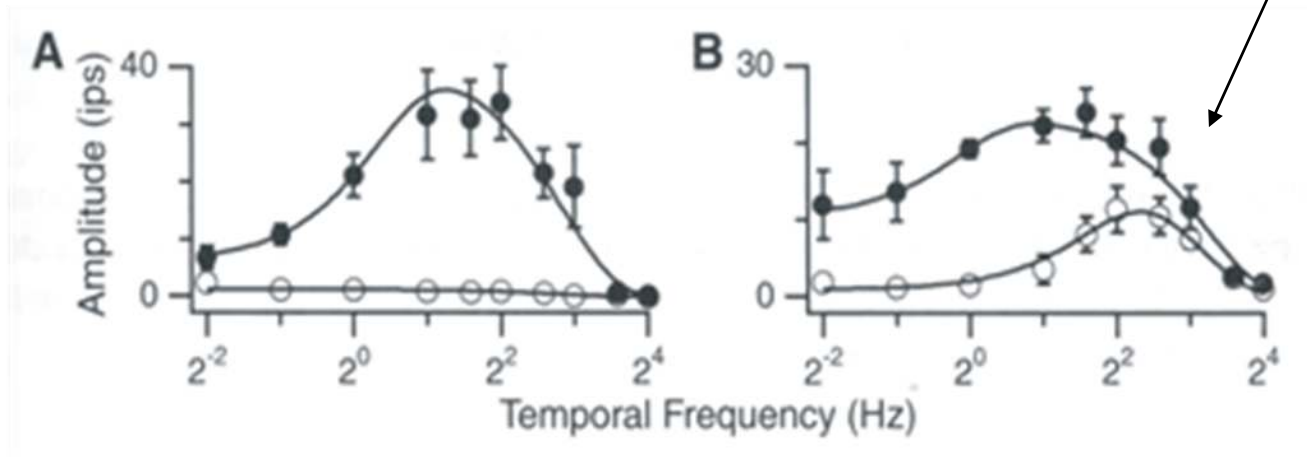
stimulus



Direction selectivity changes with the speed of stimulus

Cell 1

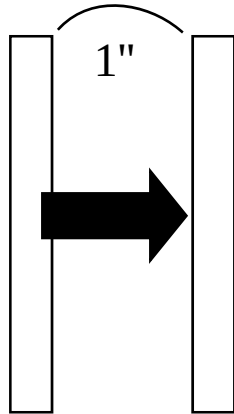
Cell 2



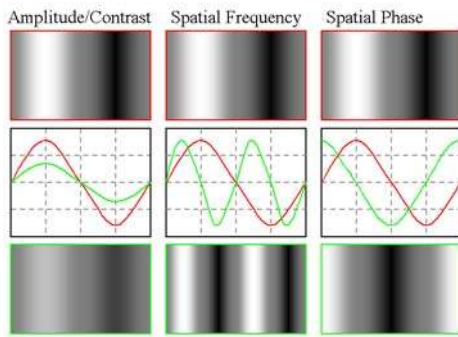
(Saul and Humphrey, 1992)

Space-time connection is the base of direction selectivity

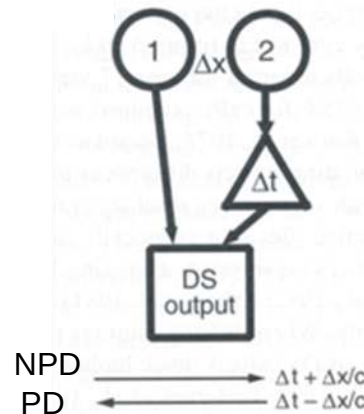
Direction selectivity is produced by local – within receptive field - interactions.



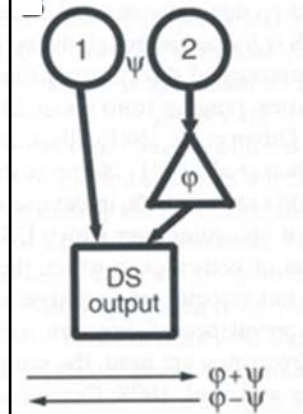
Test-stimulus



Space-time domain

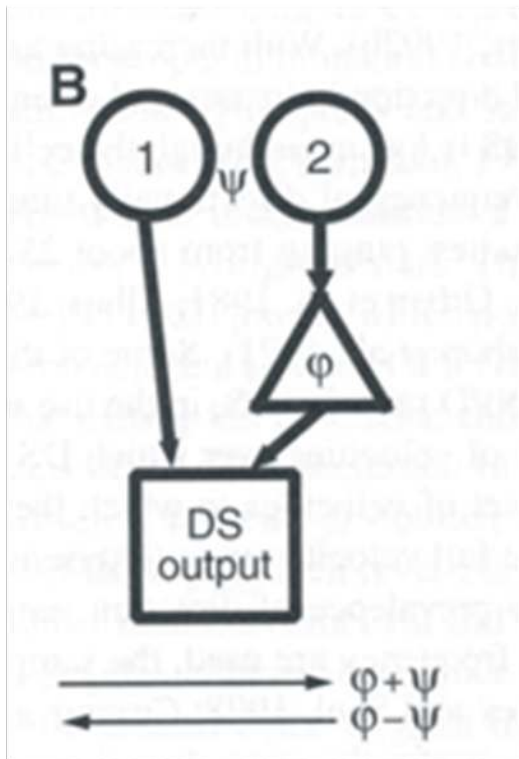


Frequency domain



Combination of inputs: inhibitory input reverses PD !!

Space-time connection in direction selectivity



One of the directions: inputs are
in opposite phase
(1/2 cycle difference)

The other direction : inputs are
in the same phase
(0 cycle difference)



ϕ and ψ mean 1/4 cycle
"spatiotemporal (ST)- quadrature"

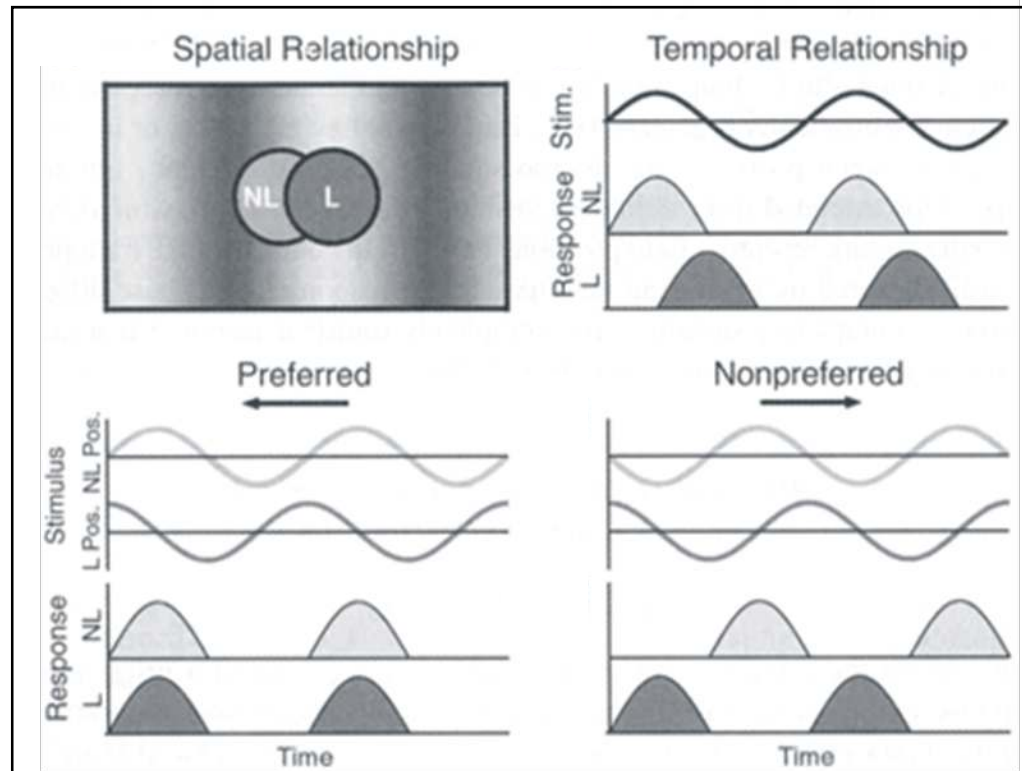
Space-time connection in direction selectivity

ideal case

ϕ and $\psi = 1/4$ cycle

(Saul and Feidler, 2002)

Spatial difference in receptive fields



Constant stimulus-
(modulated by luminance)
evoked temporal
difference in responses

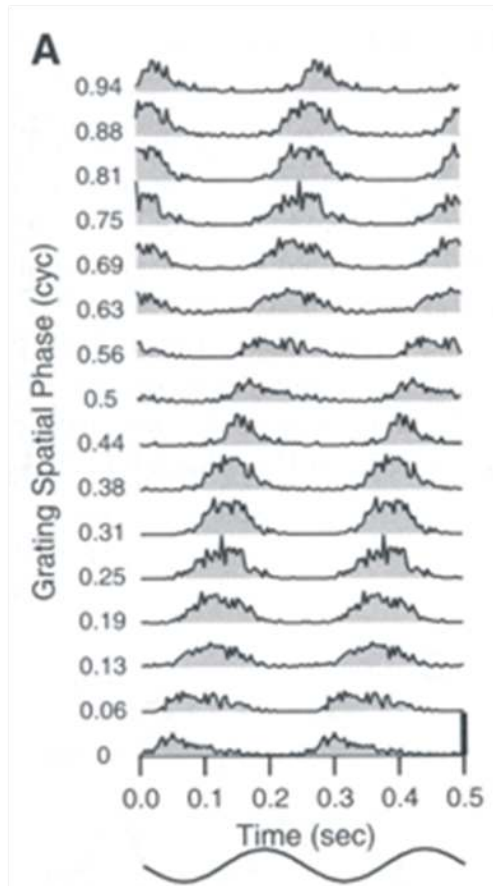
Luminance profiles of
the stimulus in the
preferred direction

Luminance profiles of the
stimulus in the NON-
preferred direction

Response profiles is the
preferred direction

Response profiles is the
NON-preferred direction

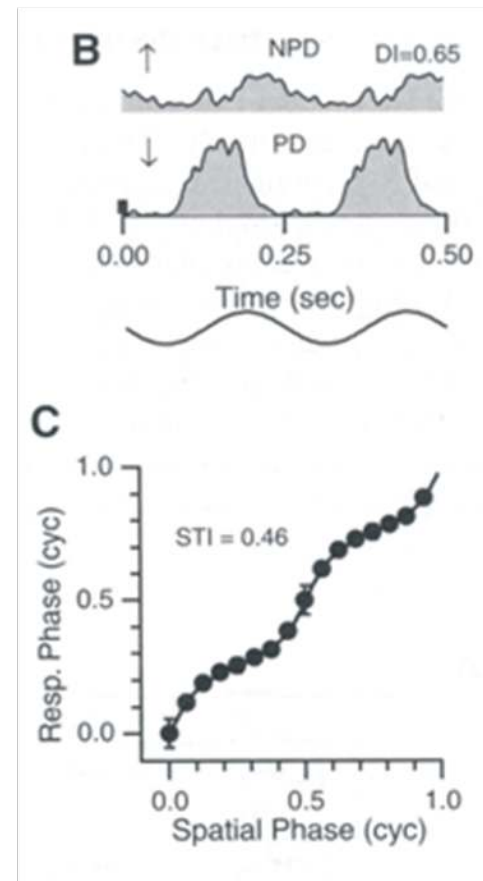
Determination of direction selectivity by spatial-temporal plots of cellular activity *(Cat, 4B layer-cell, stimulus: standing sinus waves, 4Hz)*



moving sinus-
→

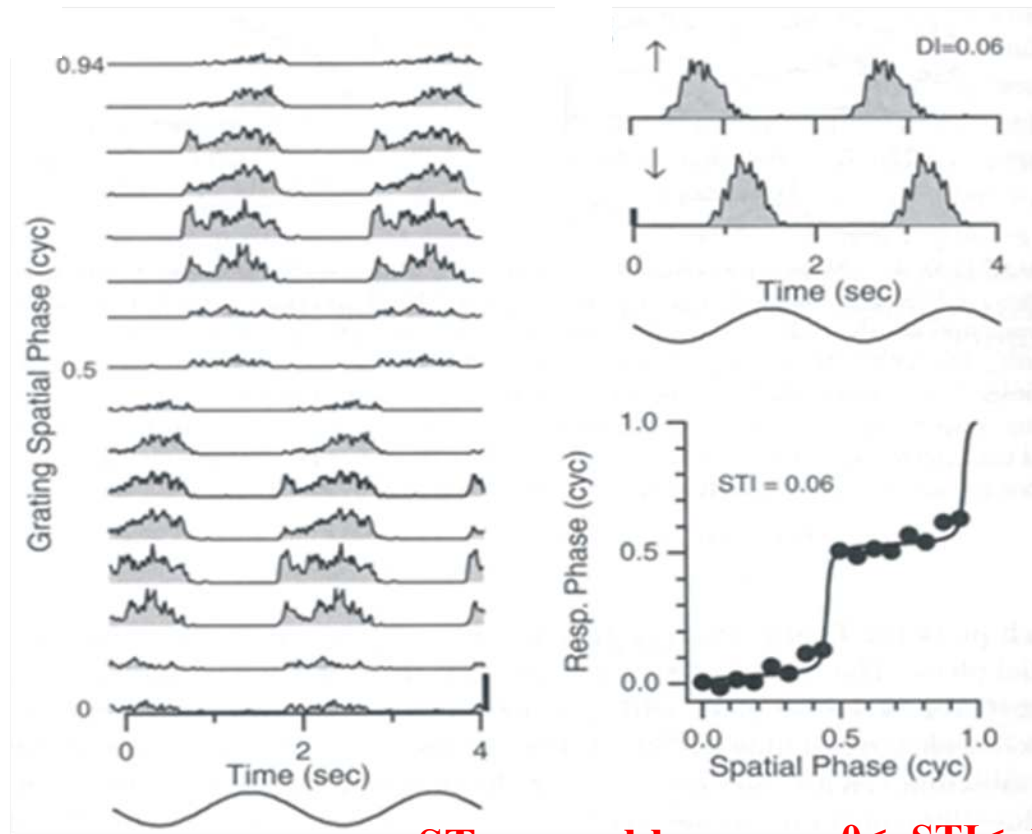
Fourier
→

ST-inseparable



(Murthy et al., 1998)

Determination of direction selectivity by means of the spatial-temporal plots of cellular activity

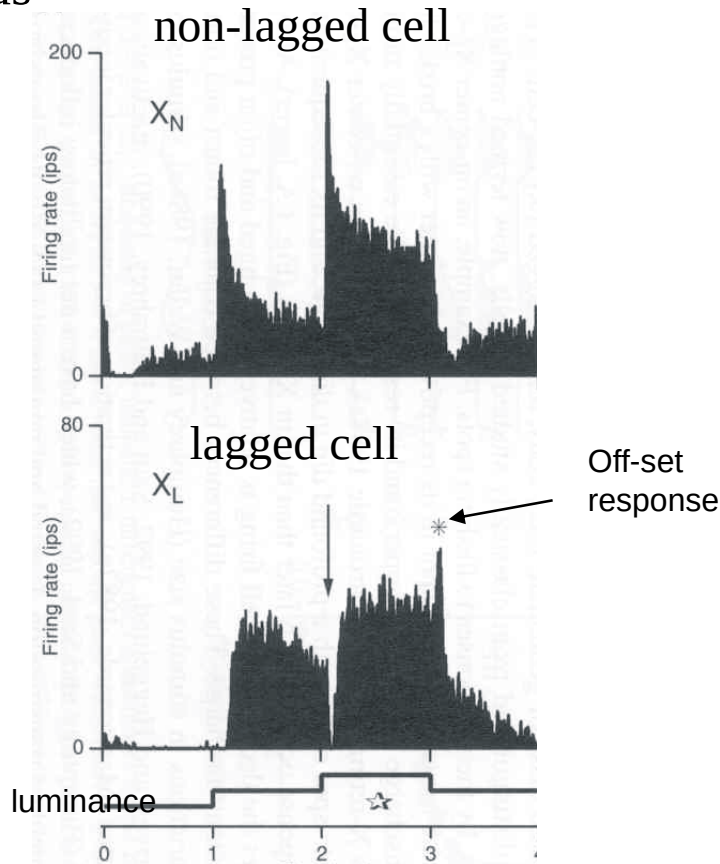


ST-separable

$0 \leq STI \leq 1$

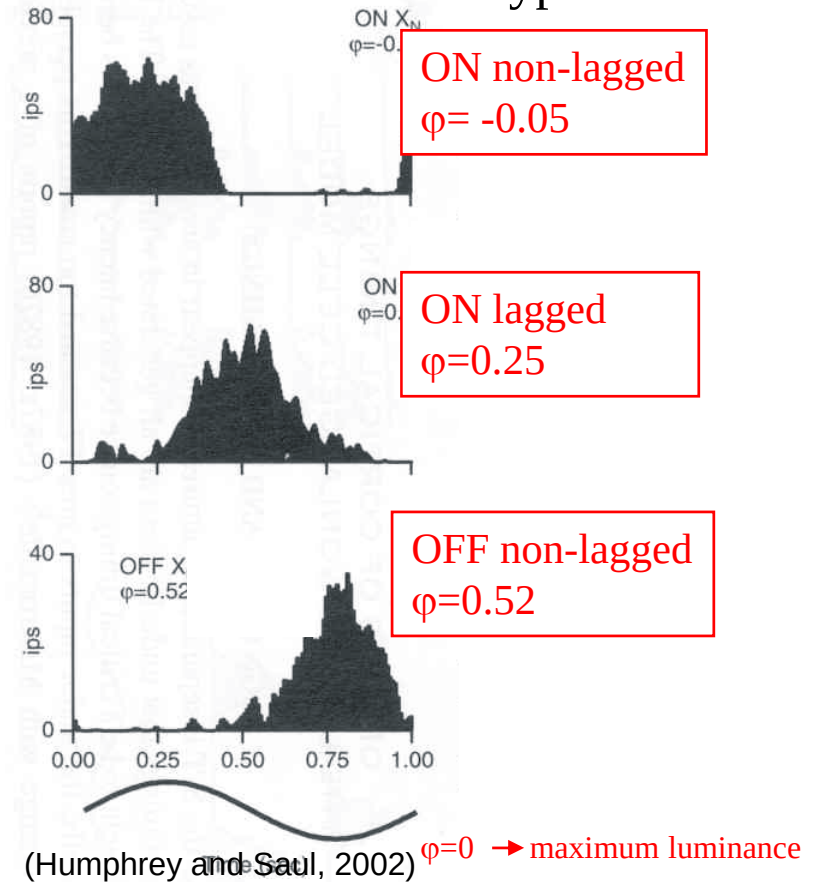
Convergence model of lagged and non-lagged cells

Thalamus



(Humphrey and Saul, 2003; Mastrorade, 1987a,b)

X-type thalamic cells



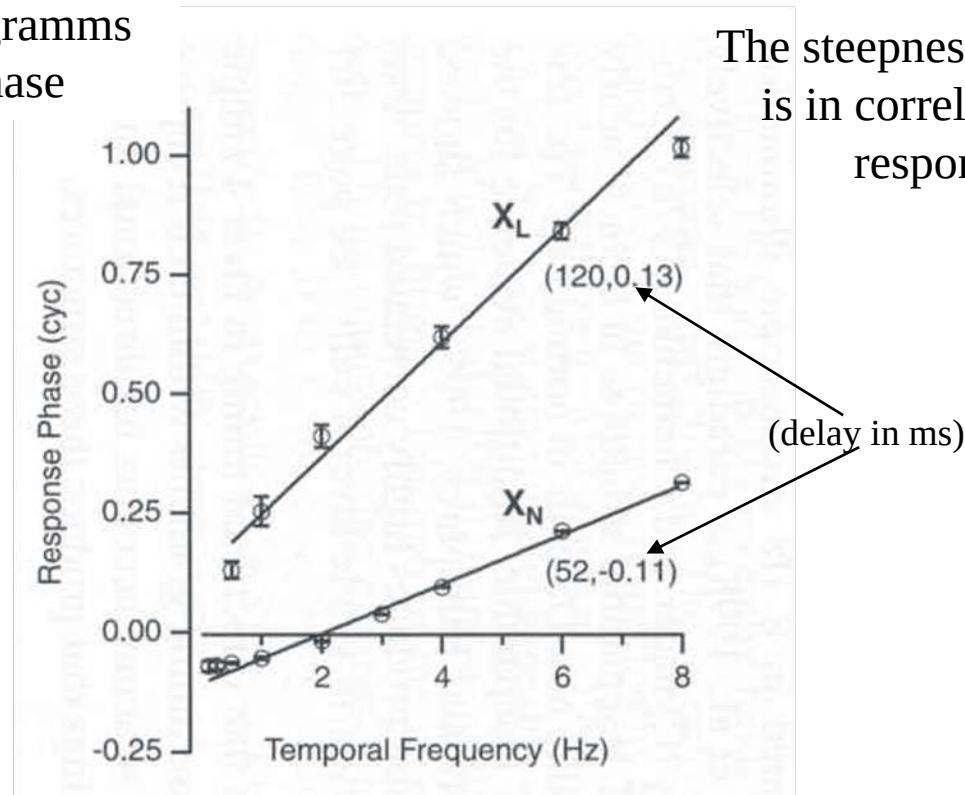
(Humphrey and Saul, 2002)

Determination of temporal differences for lagged and non-lagged thalamic cells

The crosspoints of the diagrams refer to the absolute phase

"X-lagged"
phase delay

"X-non-lagged",
phase precession



Area 17 cells: in the case of fast stimulus (>2-4 Hz) the direction selectivity is reduced or absent.

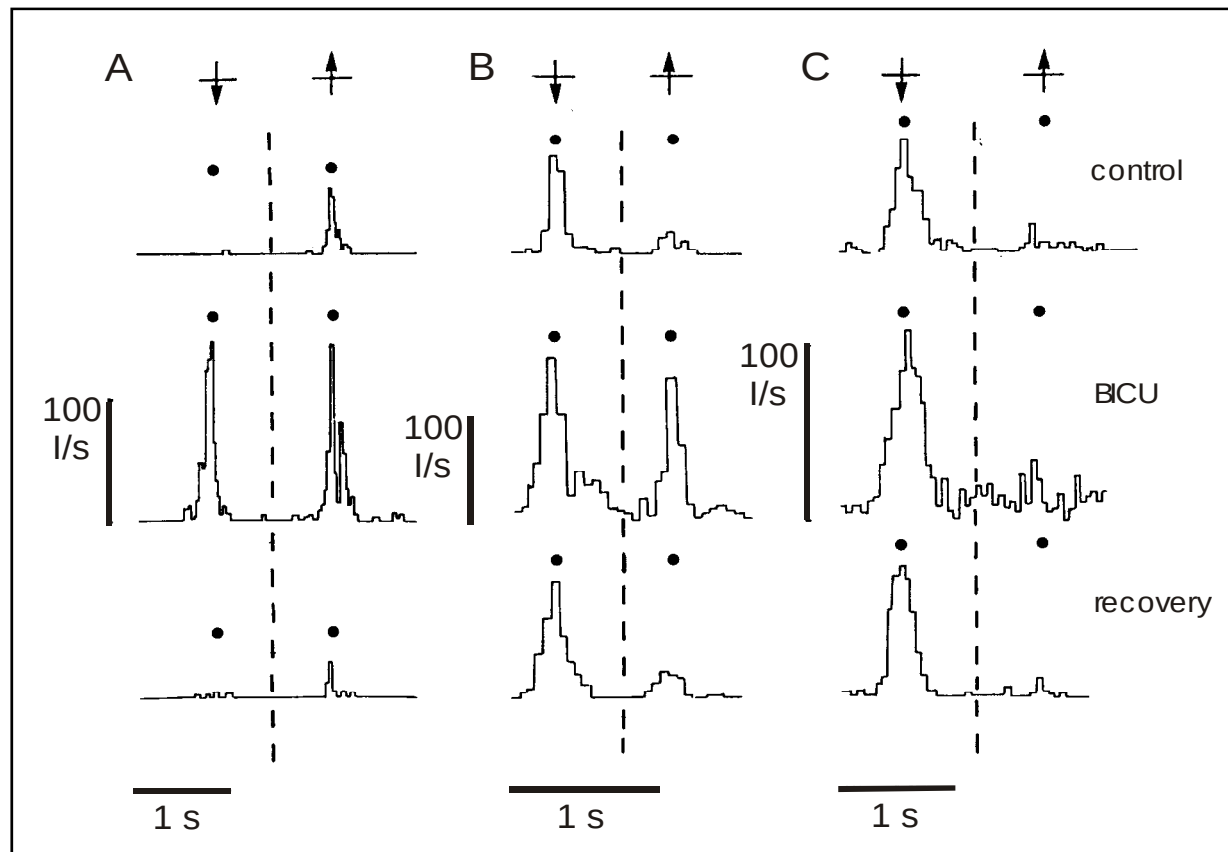
Intracortical feed-back model of direction selectivity

The essence of the model: latencies are produced by the genuine network of the cortex

- temporal activity of the thalamic input is homogenous.
(lagged, non-lagged cells are not distinguished)
- weak thalamic input (5-10% of synapses in layer 4 originates from the thalamus)
- intracortical enhancement
- excitatory elements act through receptorokon with different characteristics
(through NMDA, non-NMDA receptors: "fast and slow dynamics")
- excitatory "feed-back" connections through synaptic weight
(spatially anizotropic excitation)
- inhibition in non optimal direction ("spike thresholding")
(inhibitory cells are selective for the opposite direction)

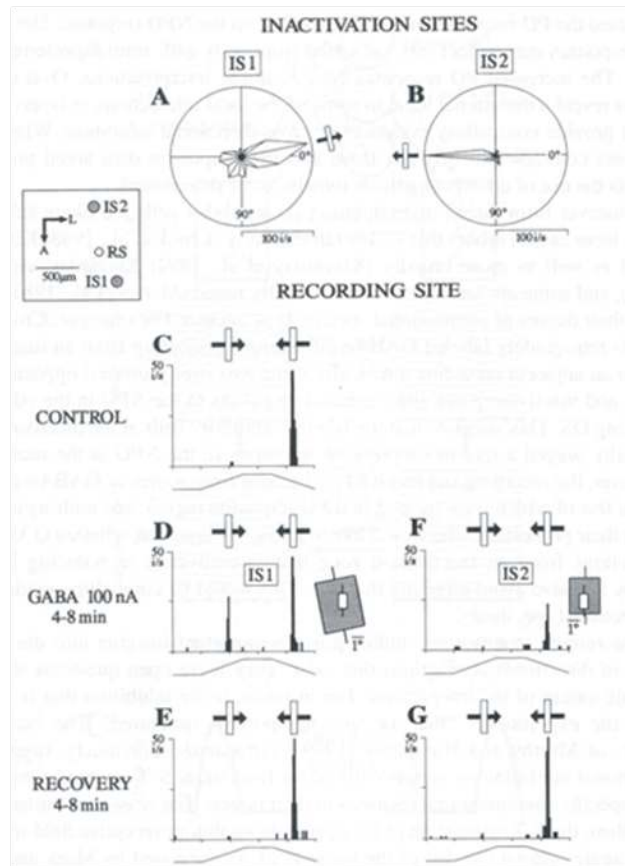
(Maex and Orban, 1996, Douglas and Martin, 1991)

Role of intracortical GABA_A inhibition in direction selectivity



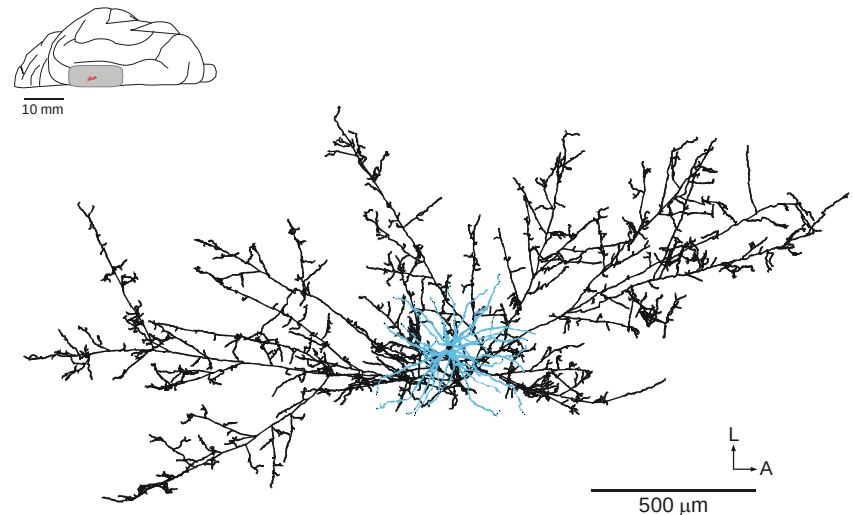
(Sillito, 1975)

Role of lateral inhibition in direction selectivity



(Crook et al., 1997)

GABAergic large basket cells
(view from the brain surface, cat area 18)



blue=dendritic tree
black=axons