The role of the neocortical laminar microcircuitry in perception, cognition, and consciousness

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Overview

- Why do we need to understand the architecture and circuitry of the brain in order to understand cognition?
- How do dynamical states in the brain map into cognitive states and ultimately into behaviour – global vs local brain processes?
- What is the role of cortical circuitry in visual hallucinations and illusions?
- What is the role of cortical circuitry in conscious visual awareness?

Why do we need to understand the architecture and circuitry of the brain in order to understand cognition?

- Computer scientists, whilst able to retrieve some of the built-in purposes of a computing machine by looking at its circuitry and electronic components, are unable to use this insight to infer anything about the software running on the machine.

- This is because the software has no impact on the hardware structure, removing the possibility of implementing functional features in the computational substrate.

- Understanding the architecture and circuitry of the brain might be expected to be more successful, because the organizational complexity of neural circuitry is the result of evolutionary and developmental processes.

- These produce highly specific connectivity patterns which are continuously updated and relate structural organization to function in a causal way.

- Thus the architecture and circuitry of the brain precisely determine the brain’s dynamical states and thus its cognitive states

How do dynamical states in the brain map into cognitive states and ultimately into behaviour?

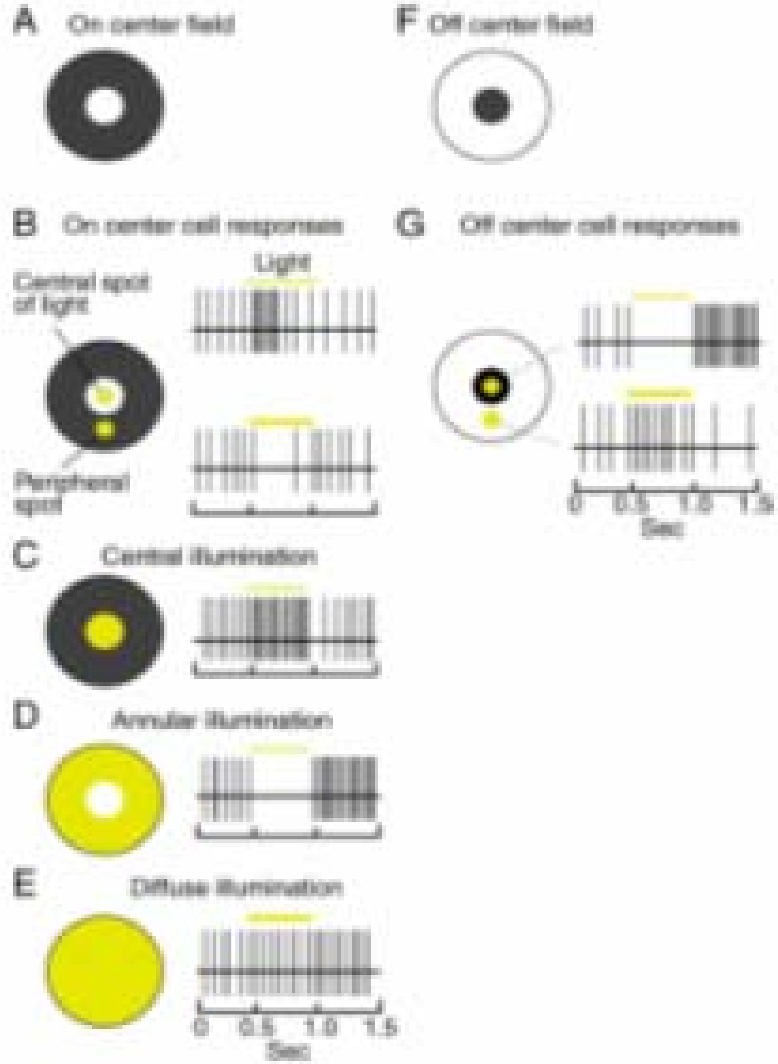
Global vs. local brain processes

- Cognition is a **global** brain process and most experiments in the brain examine **local** brain processes; ie local dynamical states. For example, in perception, the responses of neurons to local stimuli within their receptive fields

- There is a pressing need for theories, models and experimental paradigms which address the **mapping between local and global processes**, in the production of global dynamical brain states corresponding to perceptual/cognitive states

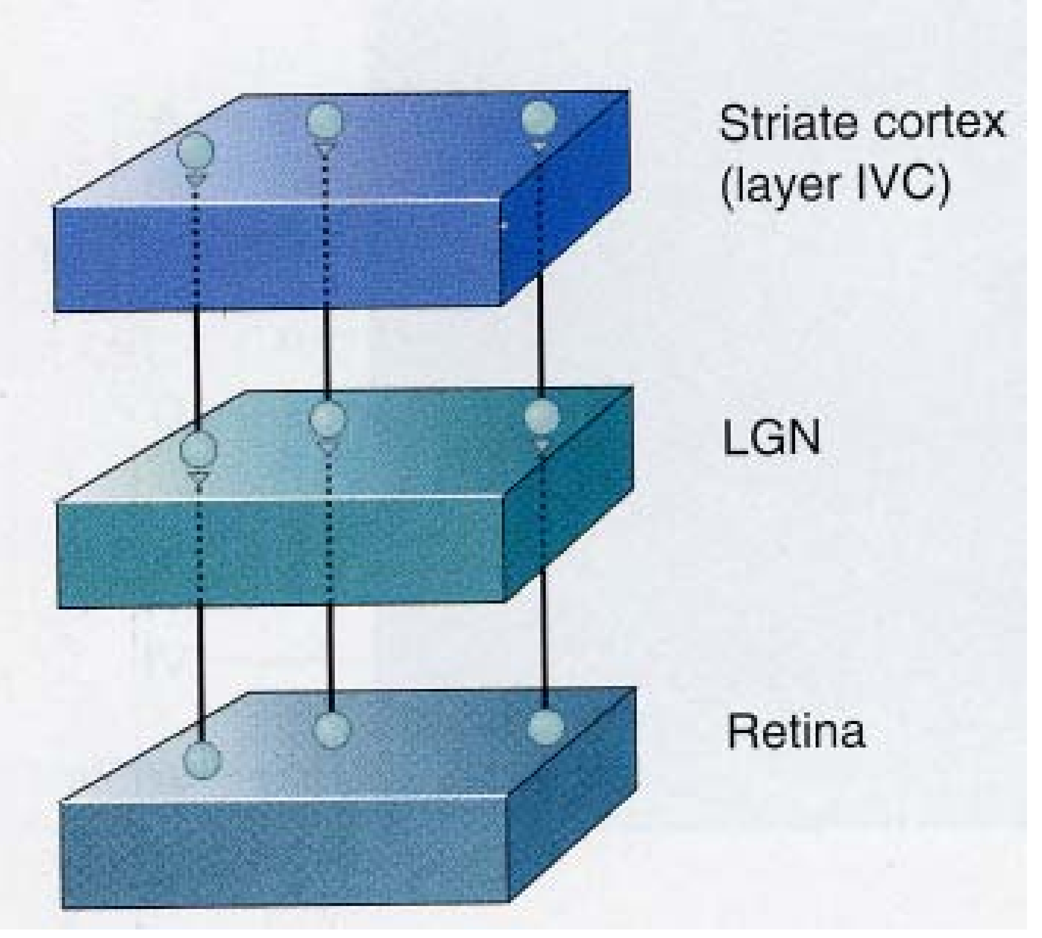
For example we know that visual stimuli are initially represented in the brain by a “mosaic” of small (less than 0.5-1° of visual space) overlapping **receptive fields** of the **retinal ganglion cells**, the axons of which form the optic nerve (1-2 million axons).

Each retinal ganglion cell is known to respond to light falling on a very small region of the retina in a precise way, by either an increase or a decrease in **the firing of action potentials**, relative to a spontaneous firing activity.

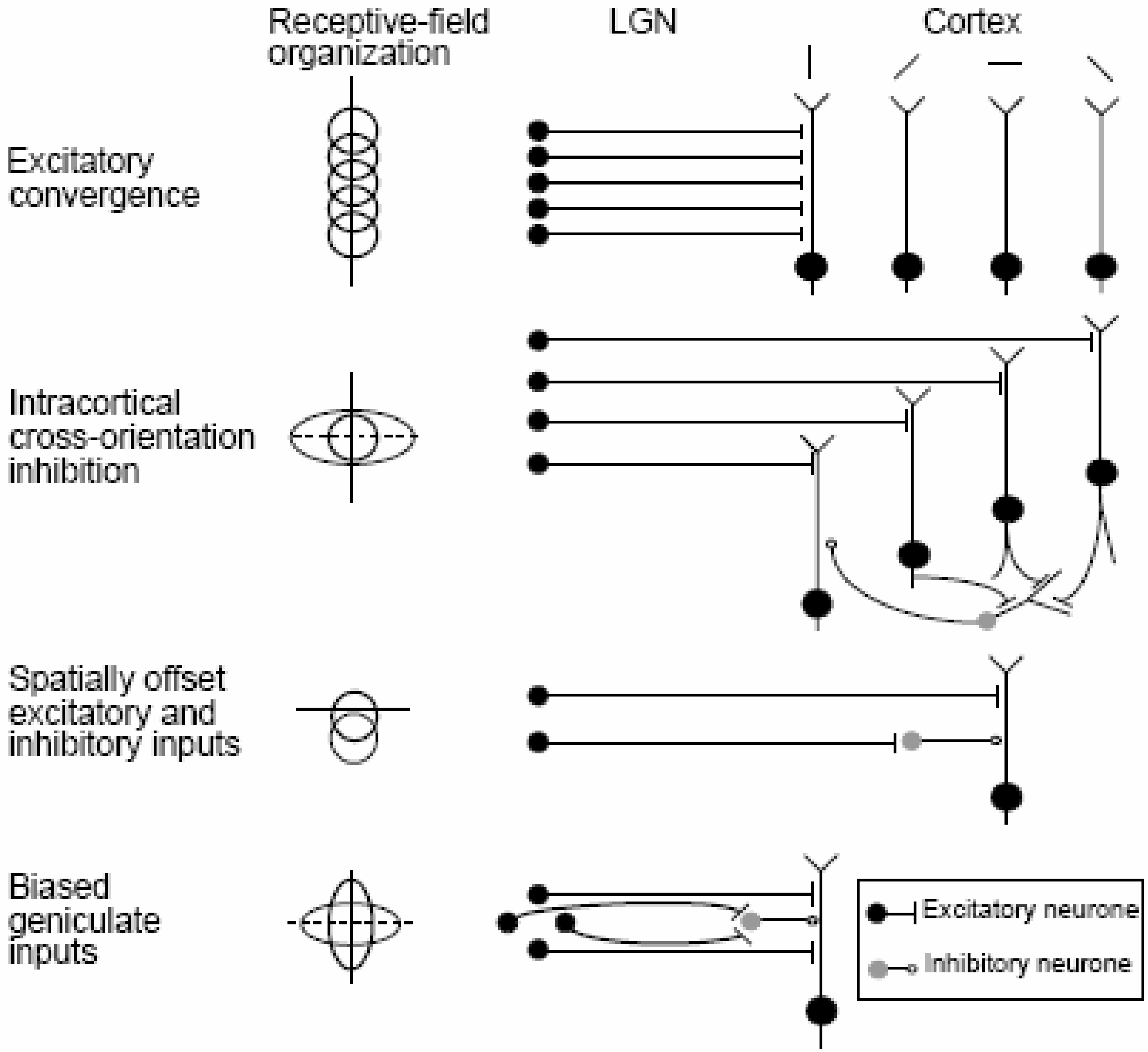


The retinal ganglion cells project on an almost **one-to-one** basis via the **optic nerve** to the **lateral geniculate nucleus** (LGN) of the thalamus, and thence to the **primary visual (striate) cortex** (V1)

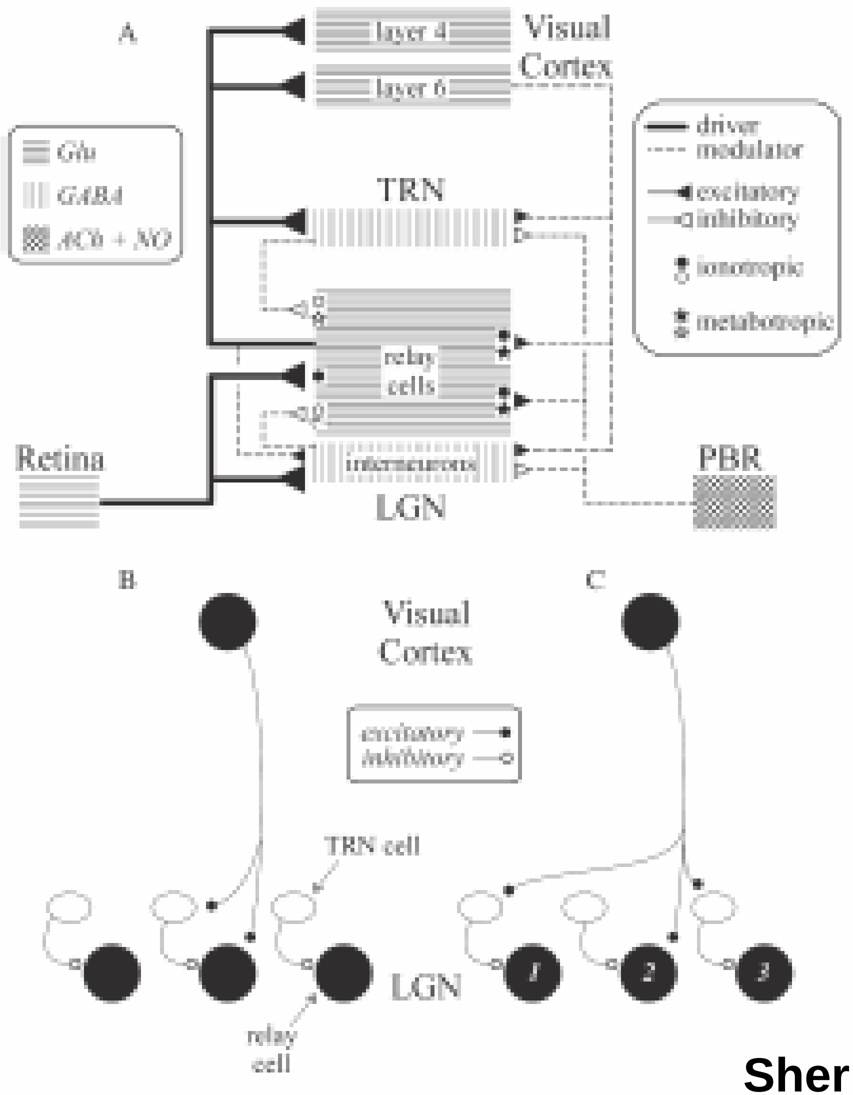
This projection is **topographic (retinotopic)** and results in a “**cortical mosaic**” of the visual stimulus in the recipient layer 4C of V1, corresponding to the receptive fields of the V1 cells



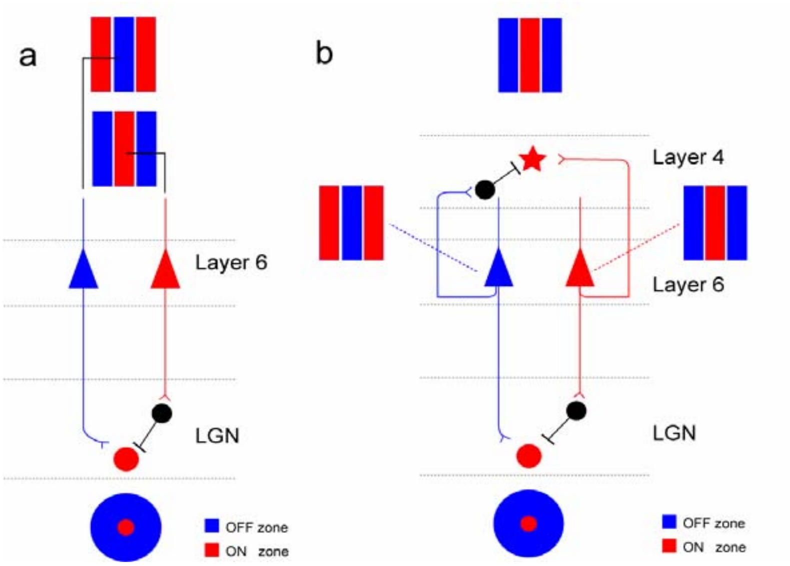
Local circuitry, both in the **feedforward projections** from LGN to V1 and in the **lateral connections** within V1 itself endow the layer 4C cortical neurons with response properties to stimuli in their receptive fields which are different to those of the retinal ganglion cells and the LGN cells.



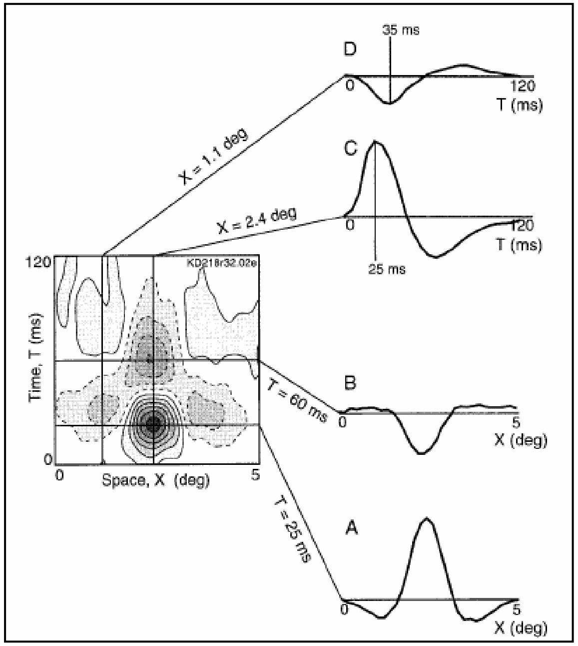
Vidyasagar et al, 1996



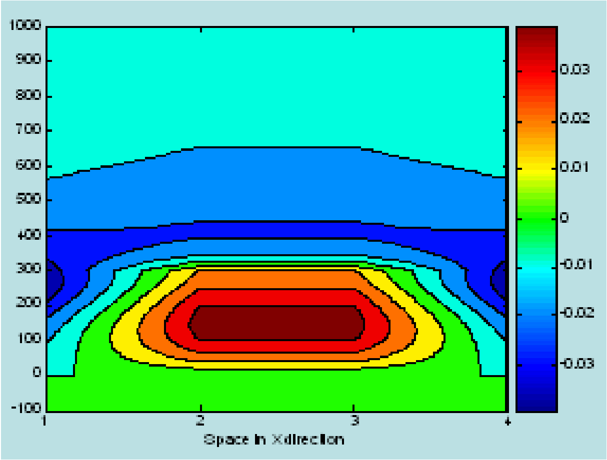
Sherman, 2005



Wang et al, 2005



Cai et al, 1997

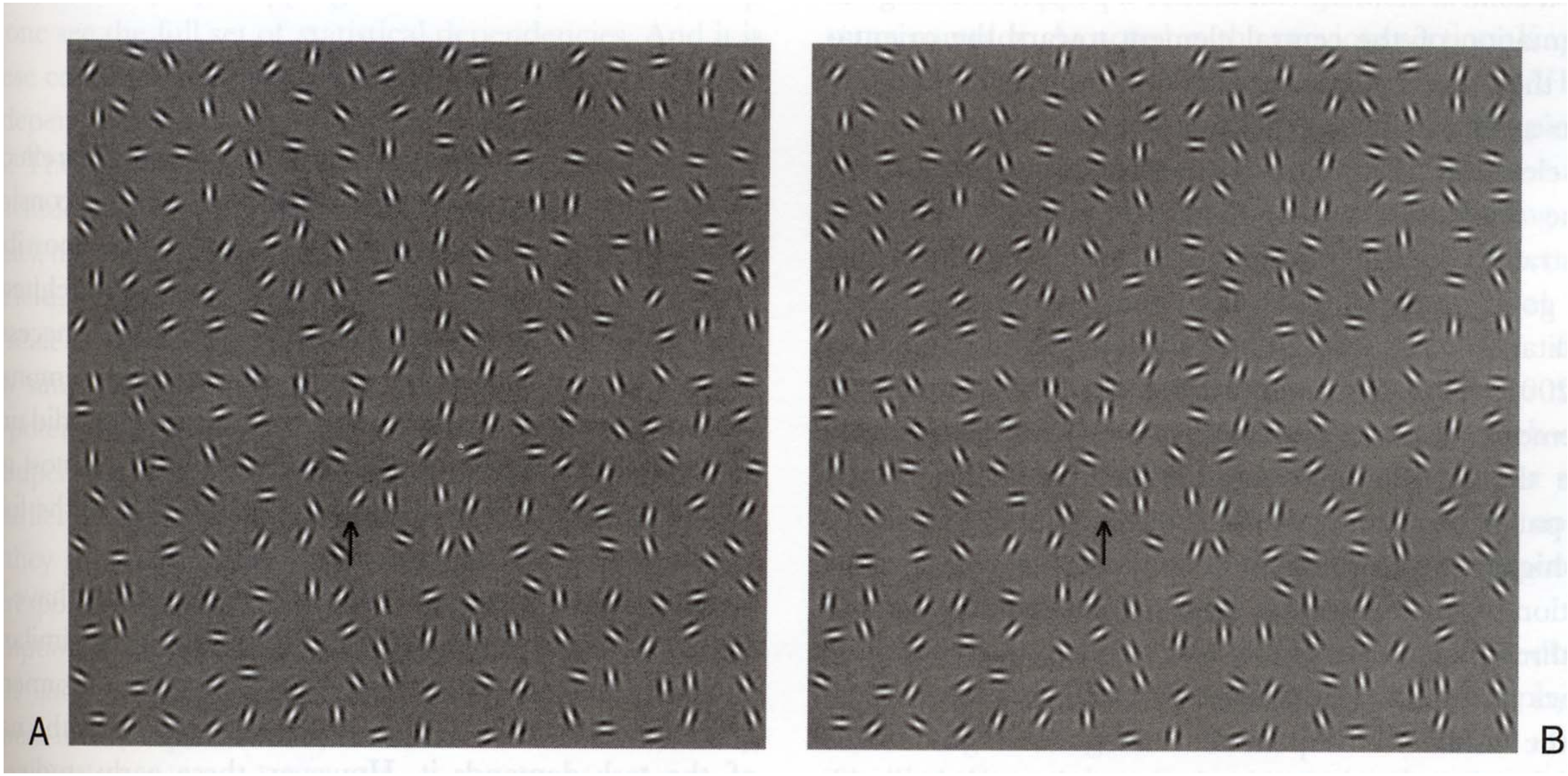


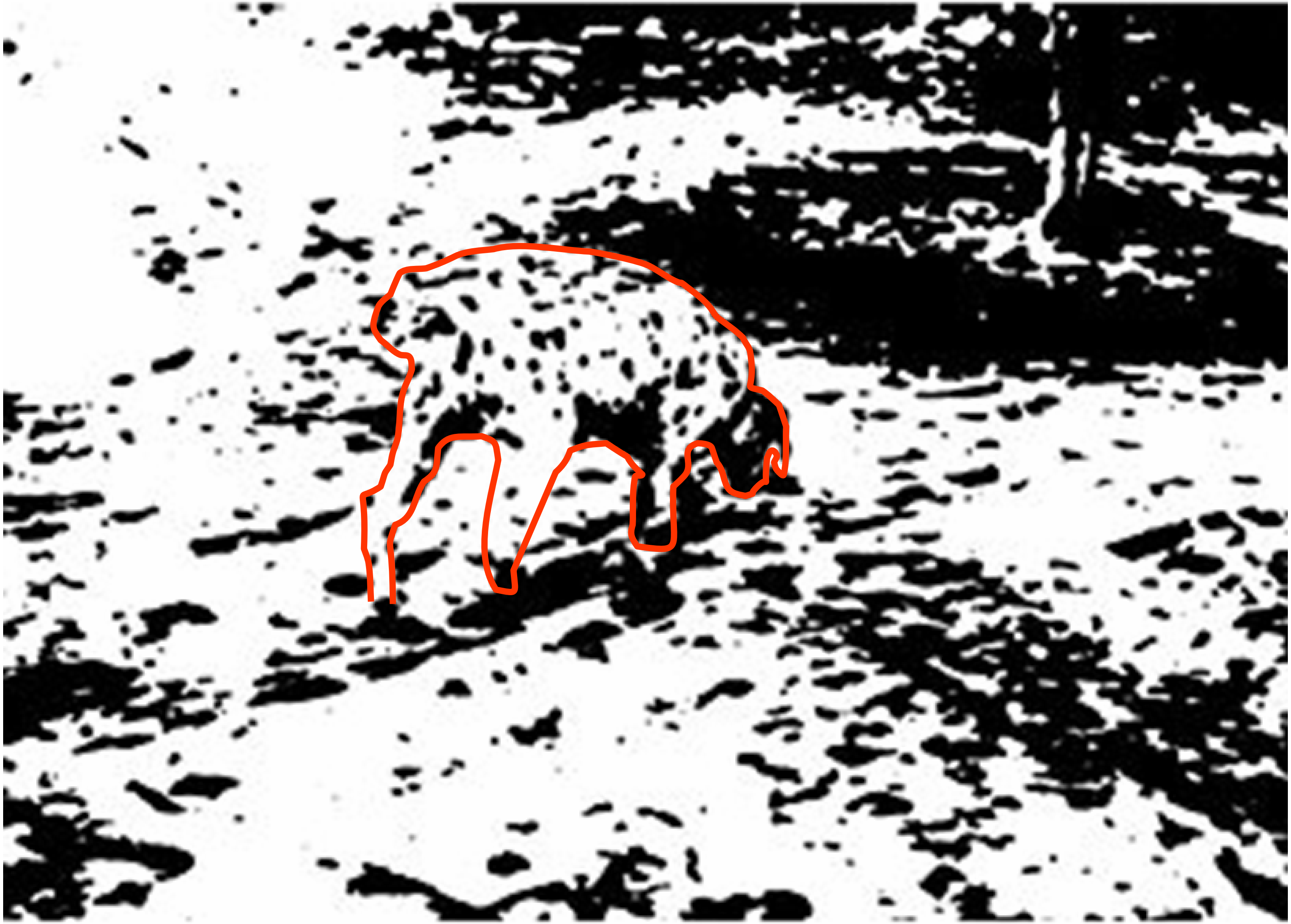
Yousif & Denham, 2006

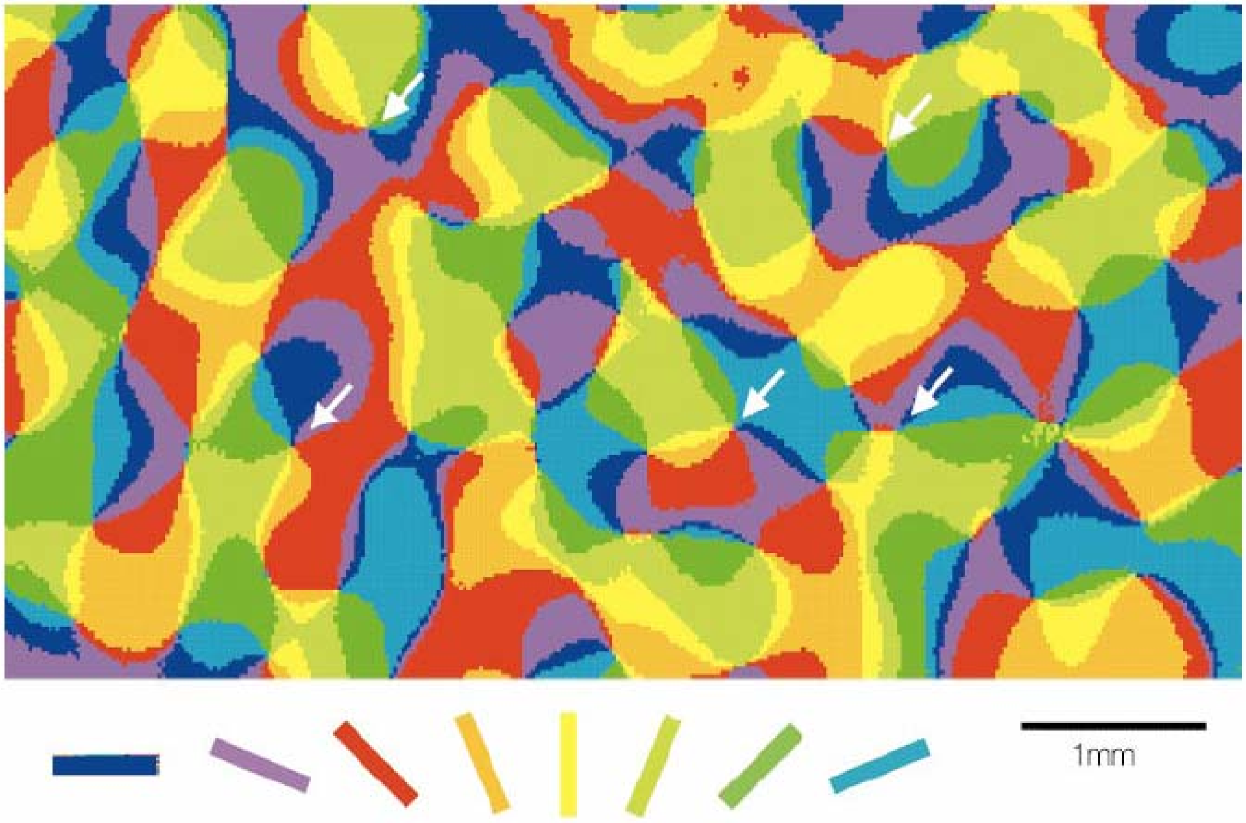
Thus layer 4C neurons have specific spatiotemporal responses which are **selective** for particular **local features** of the visual stimuli which fall within its receptive field, eg

- the **orientation** of a contrast edge of light,
- its **direction of motion**, or
- the **spatial and temporal frequency** of a set of oriented contrast edges.

But these features are still represented **locally** in the cortical mosaic formed by the receptive fields of the neurons in V1 – how then do we perceive **global contours** made up from a set of local orientated contrast edges?


A
B

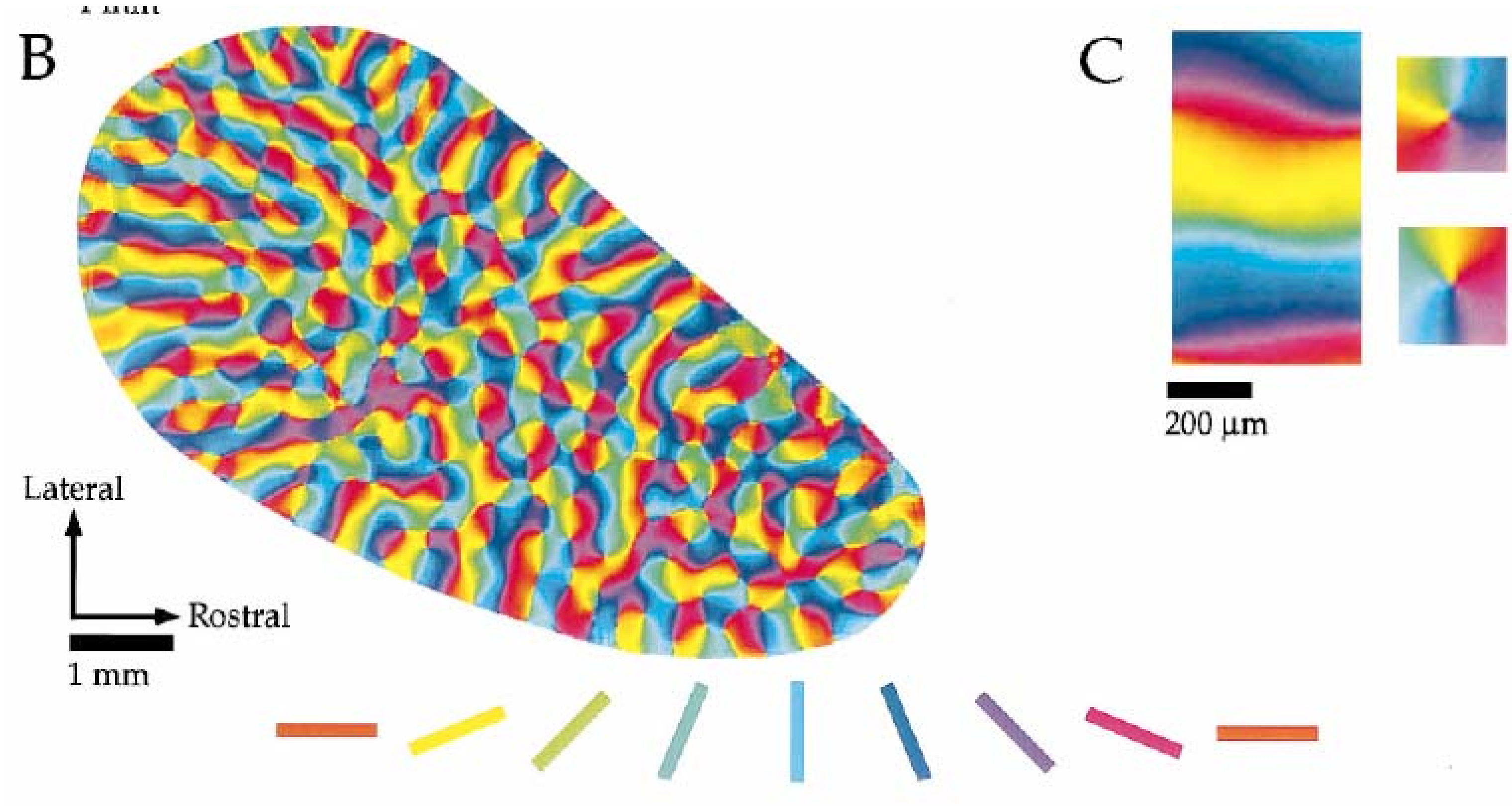




Eysel, Nature, 1999

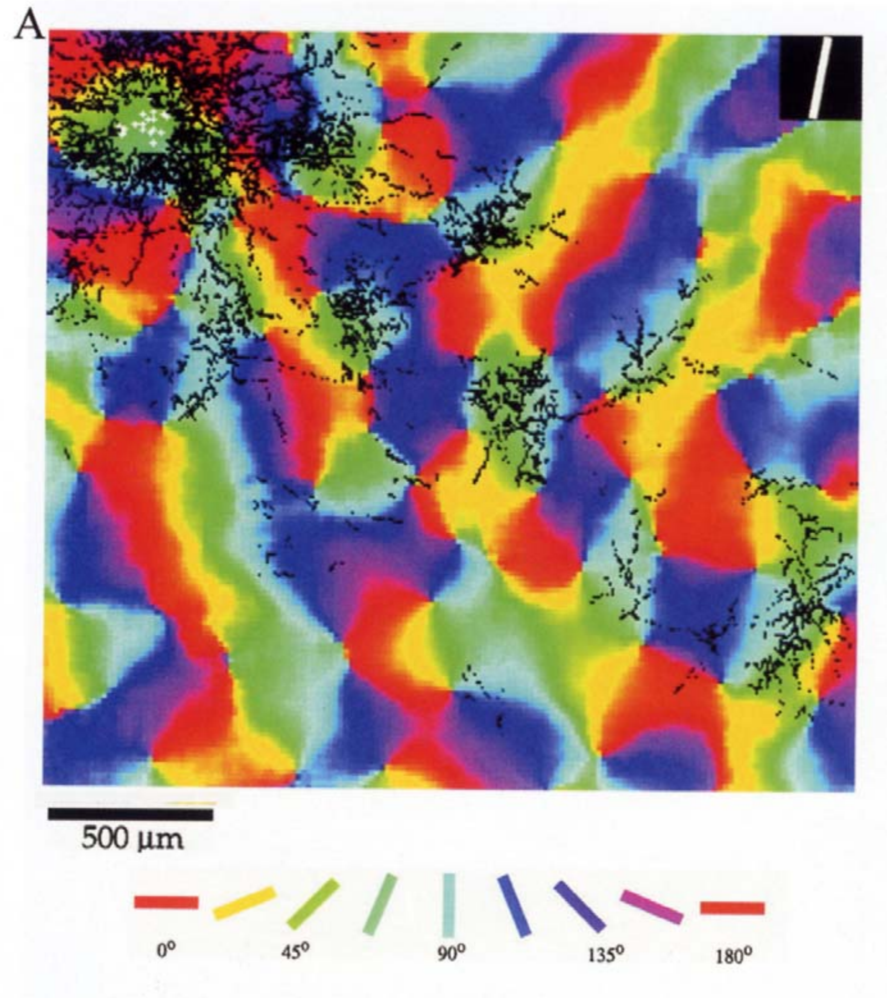
Orientation selectivity in layer 2/3 is organised into **orientation columns** – regions of cortex within which the neurons share the **same orientation preference**.

Changes in orientation preference are **continuous** across columns, except at so-called **“pinwheel centres”** (arrowed)

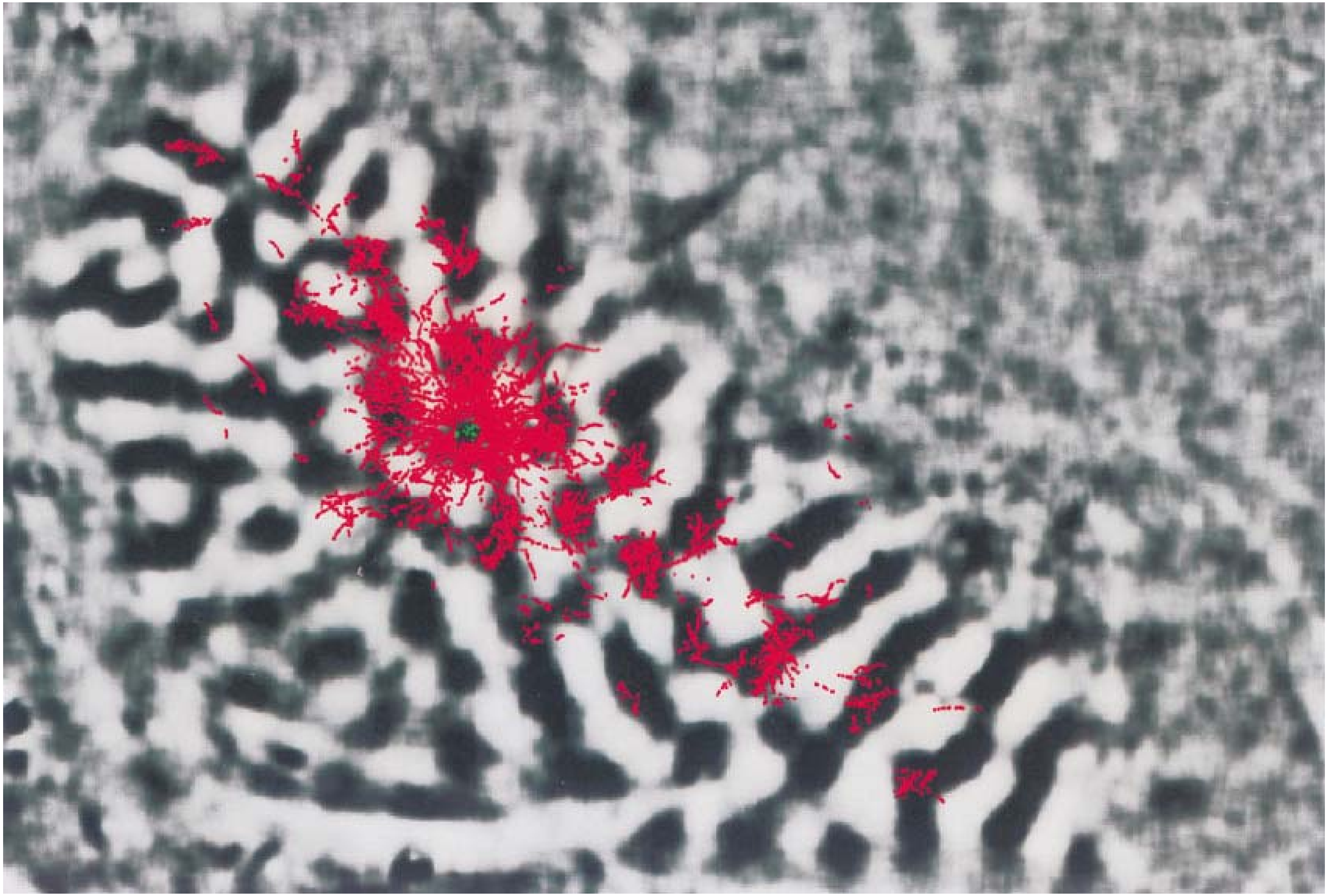


Orientation preference map in the tree shrew – Bosking et al, J Neurosci, 1997

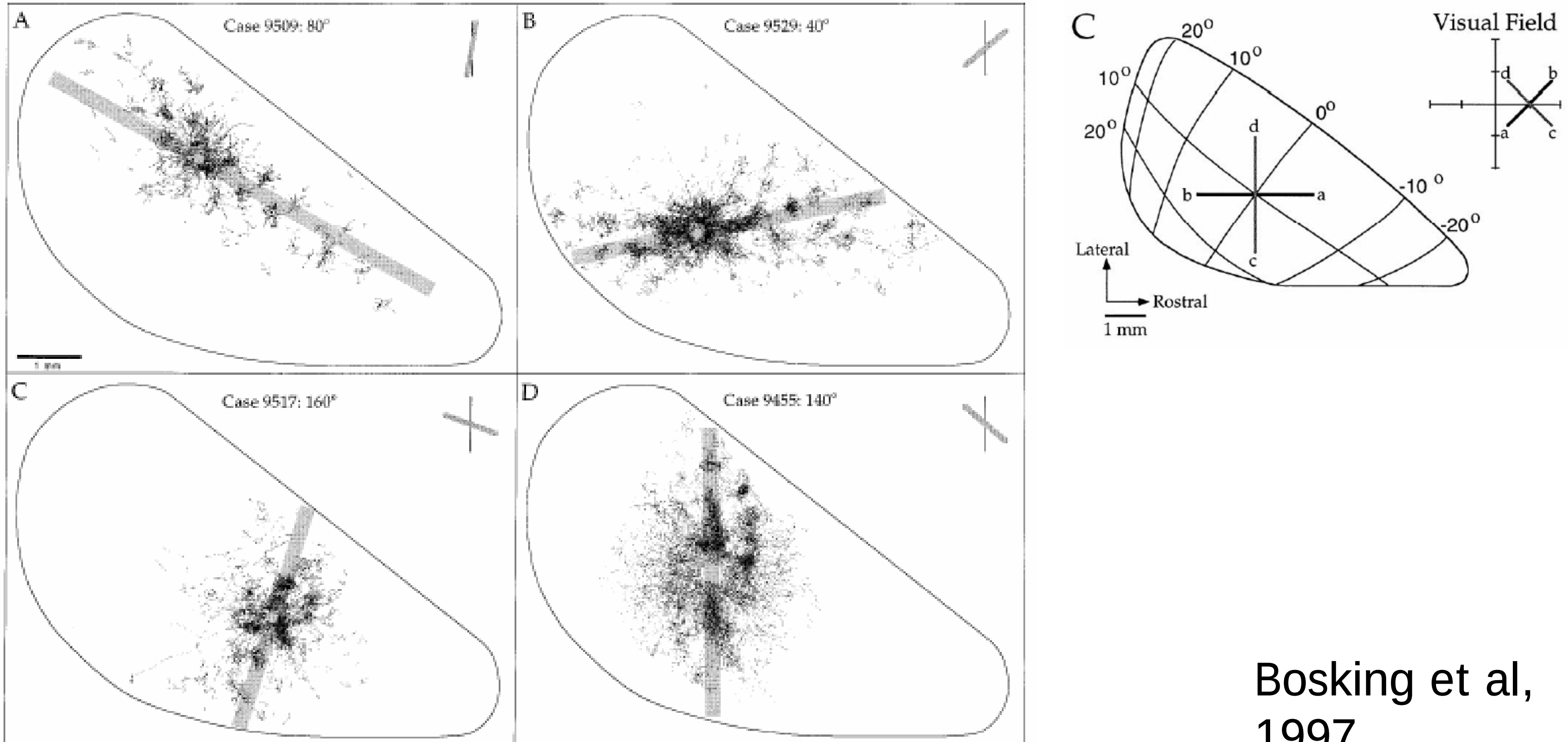
Neurons with the same orientation preference are connected by excitatory connections, horizontally (laterally) across 2-3mm of cortex



Bosking et al, 1997



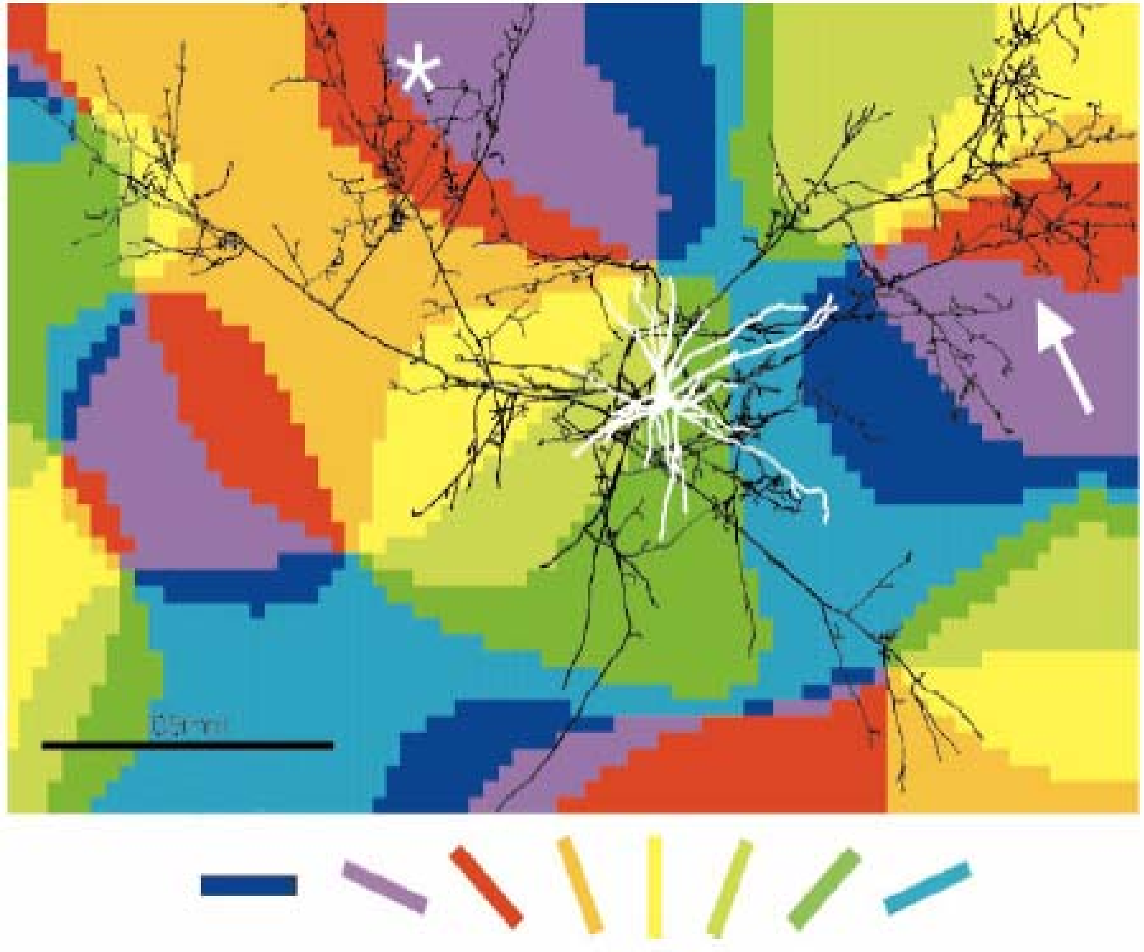
Bosking et al, 1997



Bosking et al, 1997

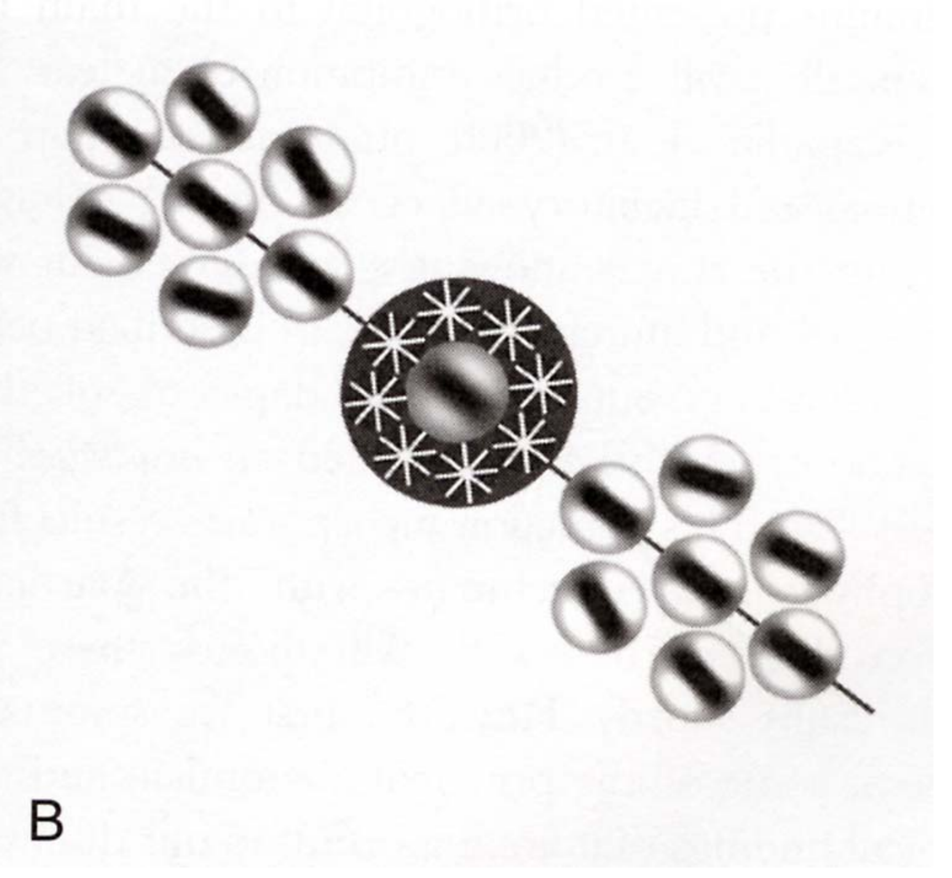
The distribution of terminal sites of the long range connections is elongated along an axis that corresponds to the preferred orientation of the neurons at the injection site

Layer 2/3 inhibitory cell (soma and dendrites in white, and the axonal distribution in black) targets regions of similar as well as orthogonal orientation preferences over distances of up to 1 mm



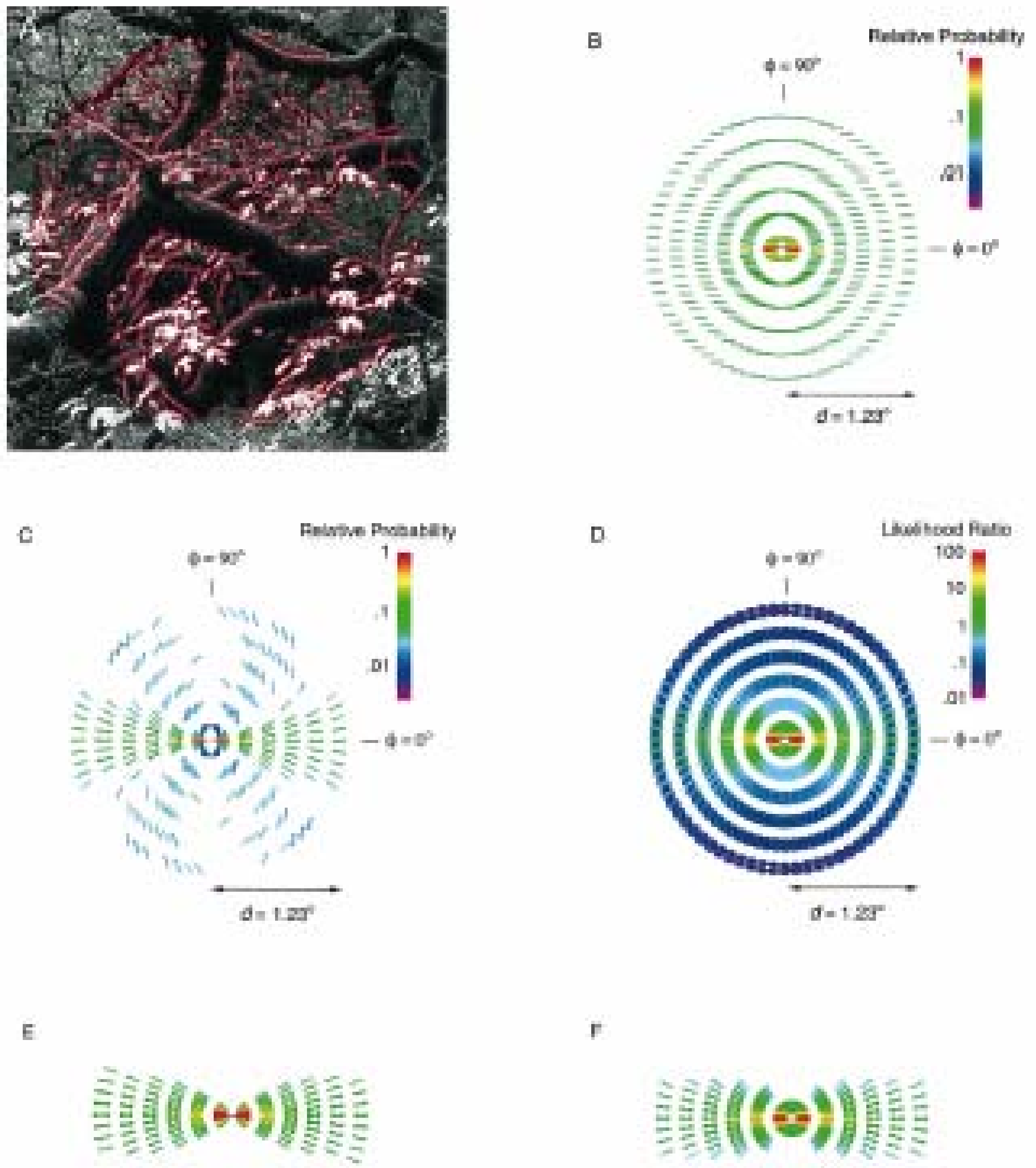
Eysel, Nature, 1999

A combination of non-orientation selective local inhibitory connections and orientation-aligned long-range excitatory connections provide the basis for increased responses of neurons in V1 to contours made up of approximately co-aligned local edges – so-called “association field” (Field et al, Vision Res, 1993)



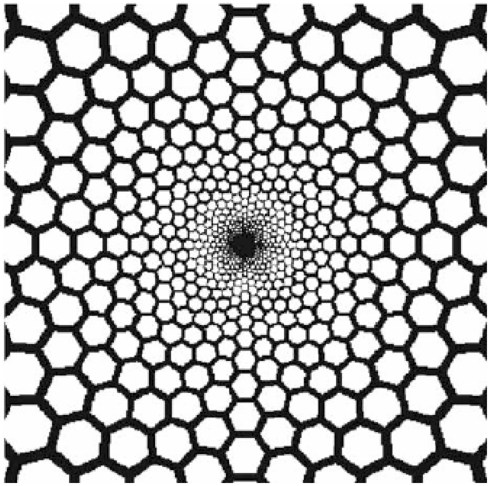
Field & Hayes, Visual Neurosciences, 2004

The observed cortical circuitry closely matches **grouping** functions derived from the statistics of spatial relationships of edges in natural images

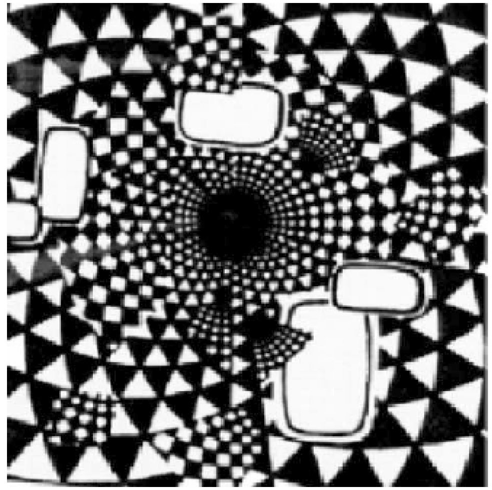


Geisler et al, Vision Research 2001

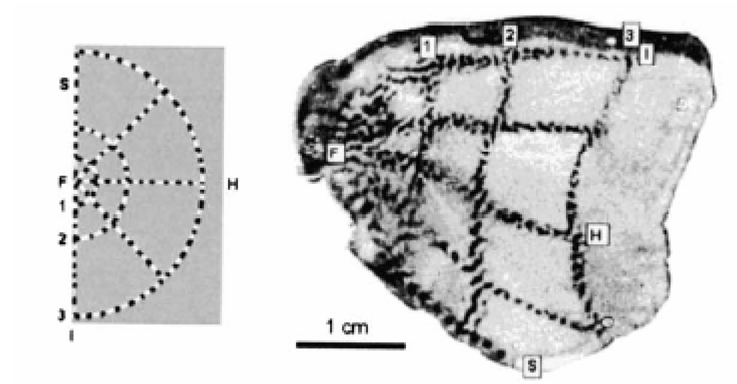
What is the role of cortical circuitry in visual hallucinations and illusions?



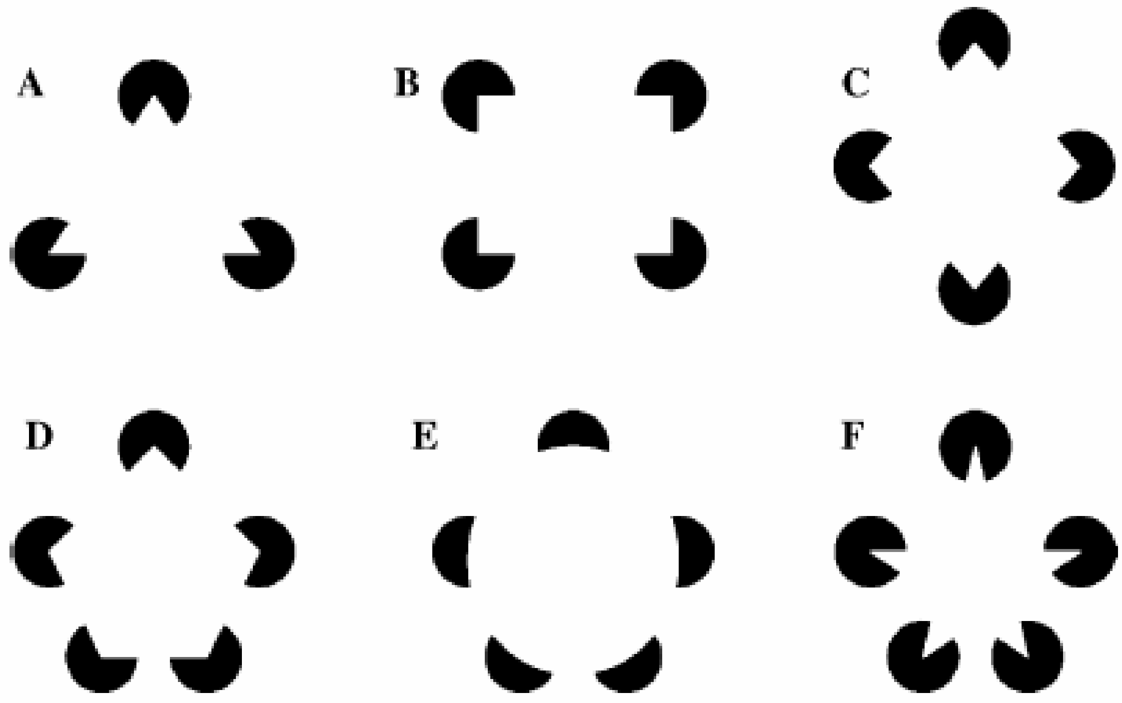
Bressloff et al, 2002



Tyler, 1978

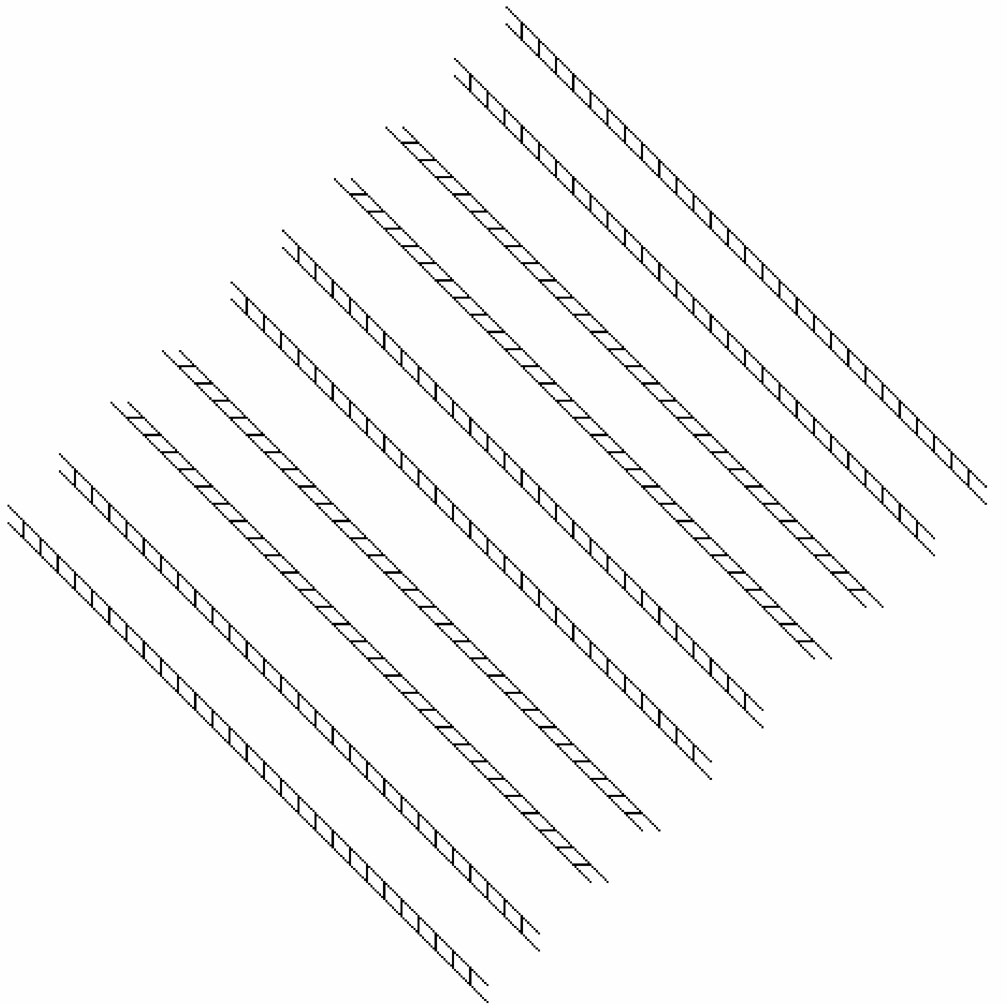


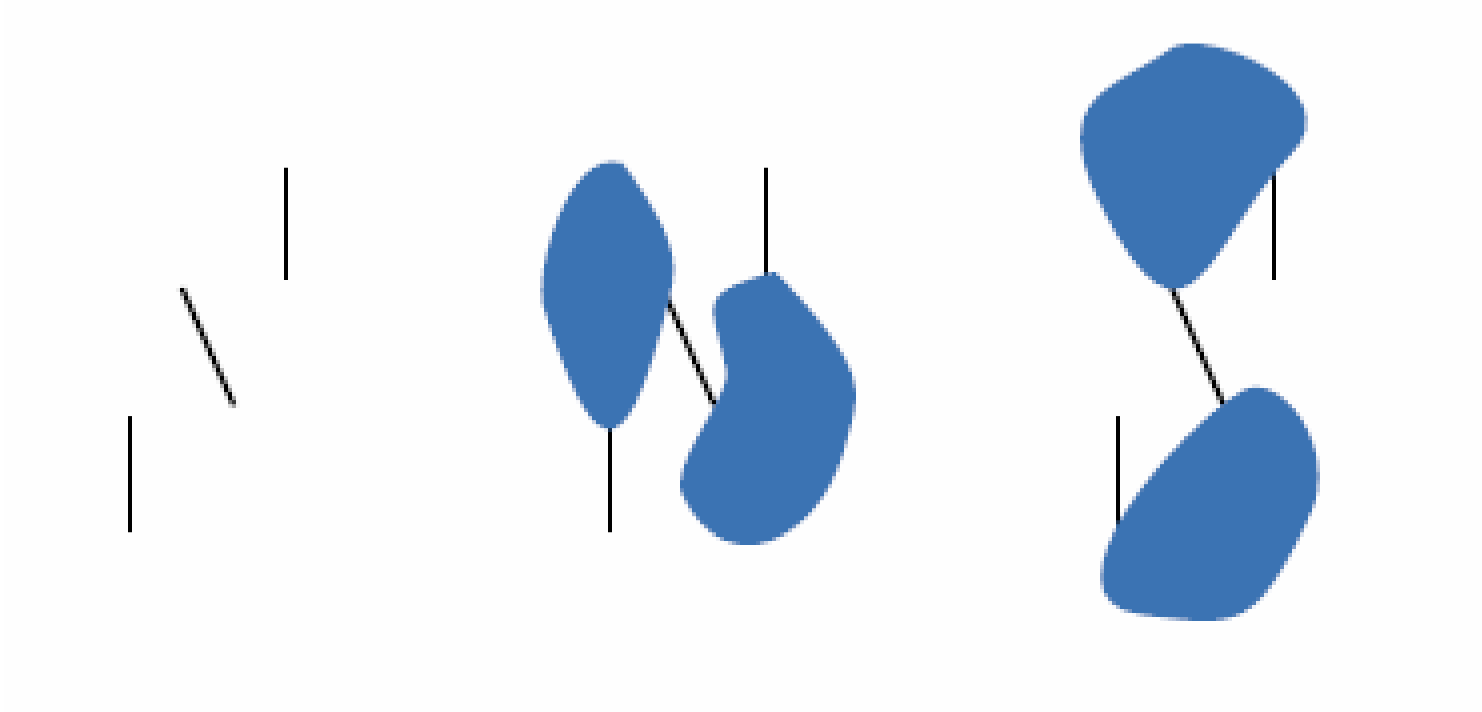
The structures typically seen in visual hallucinations, ie funnels, honeycombs, spirals, and cobwebs, can be seen in the nonlinear dynamical behaviour (planforms) of the primary visual cortex, when this is mapped into the visual space via the log-polar mapping from the retina to the cortex (Bressloff et al, 2001).



Seghier & Vuilleumier, 2006

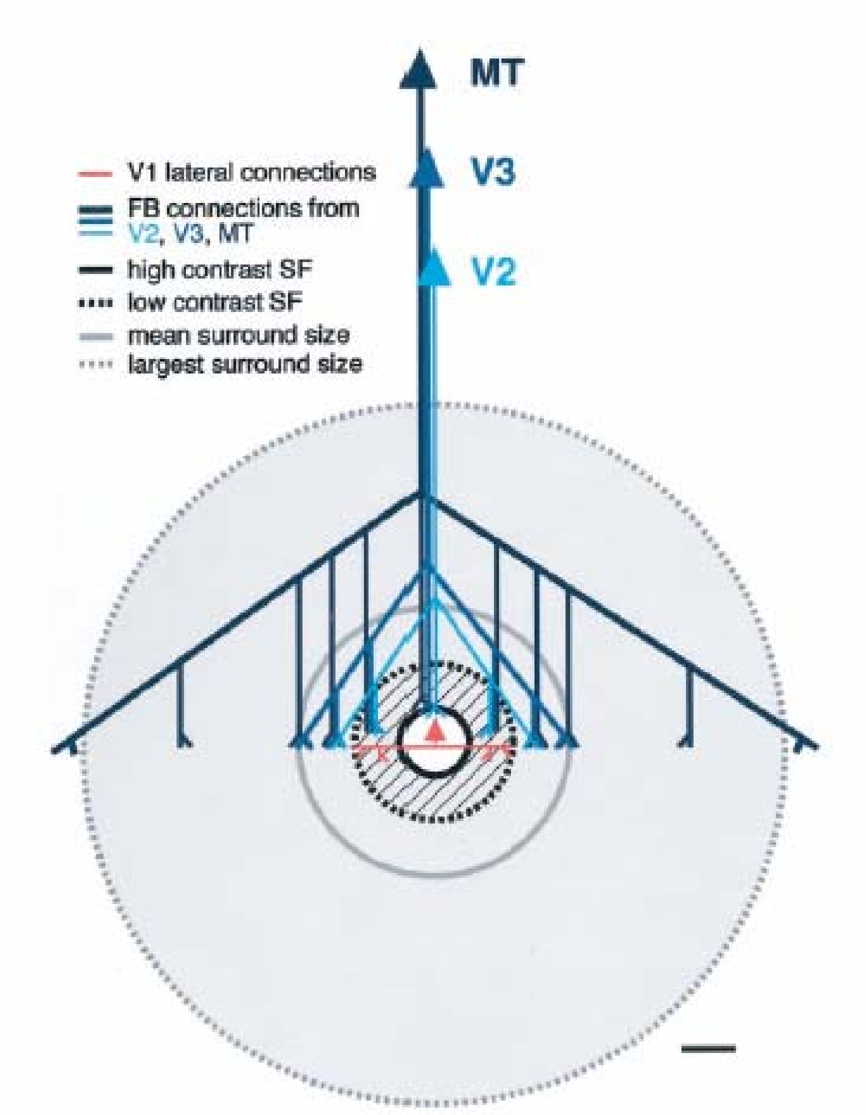
The contrasting edges of the “pacmen” at the corners give the illusion of shape, showing that cortical processing “fills in“ the edges of the shape. A likely mechanism is the long-range excitatory lateral connections in V1 which reinforce locally edges of the same orientations.





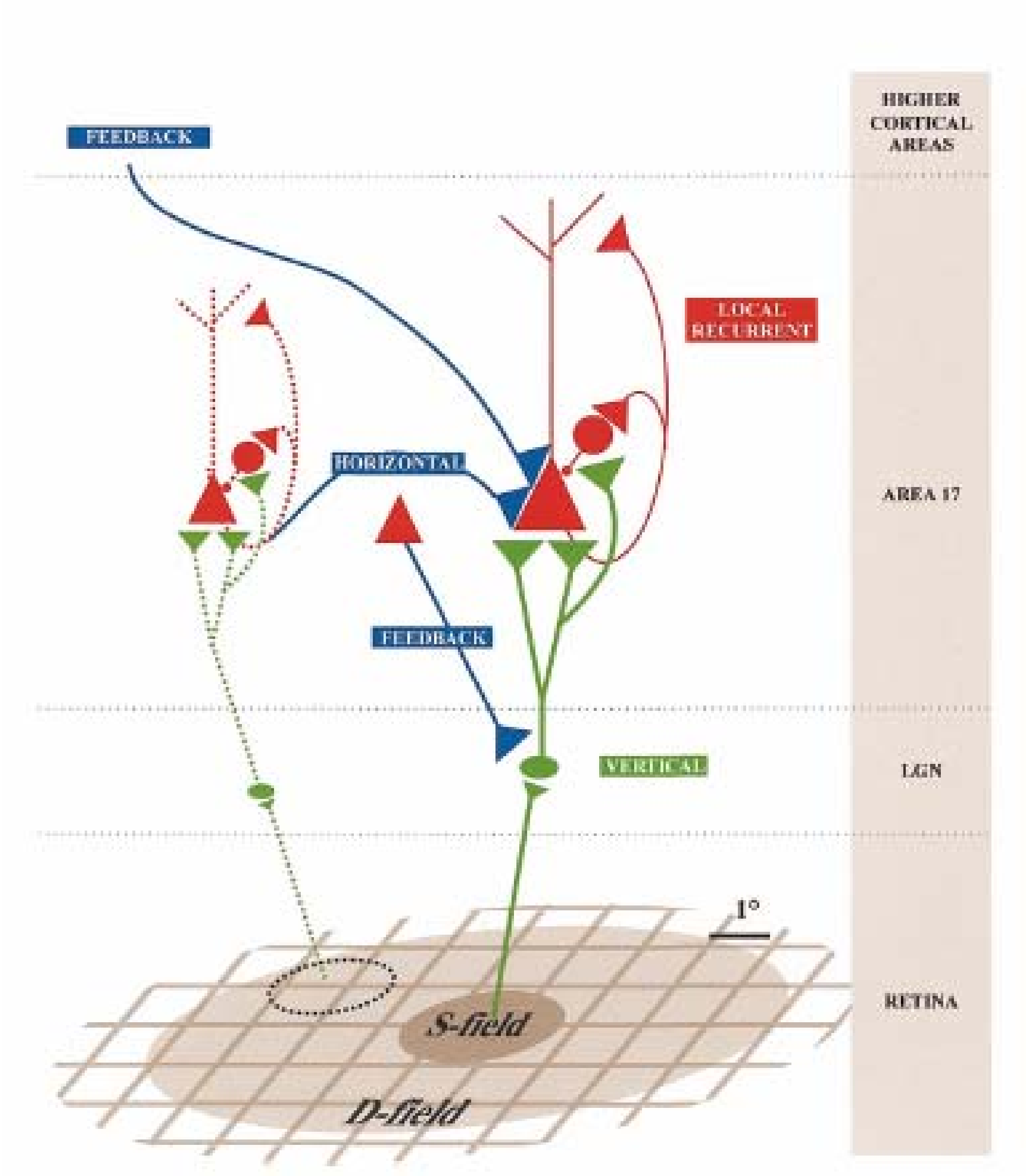
Olshausen & Field, 2005

Contour completion also depends on figure-ground segmentation

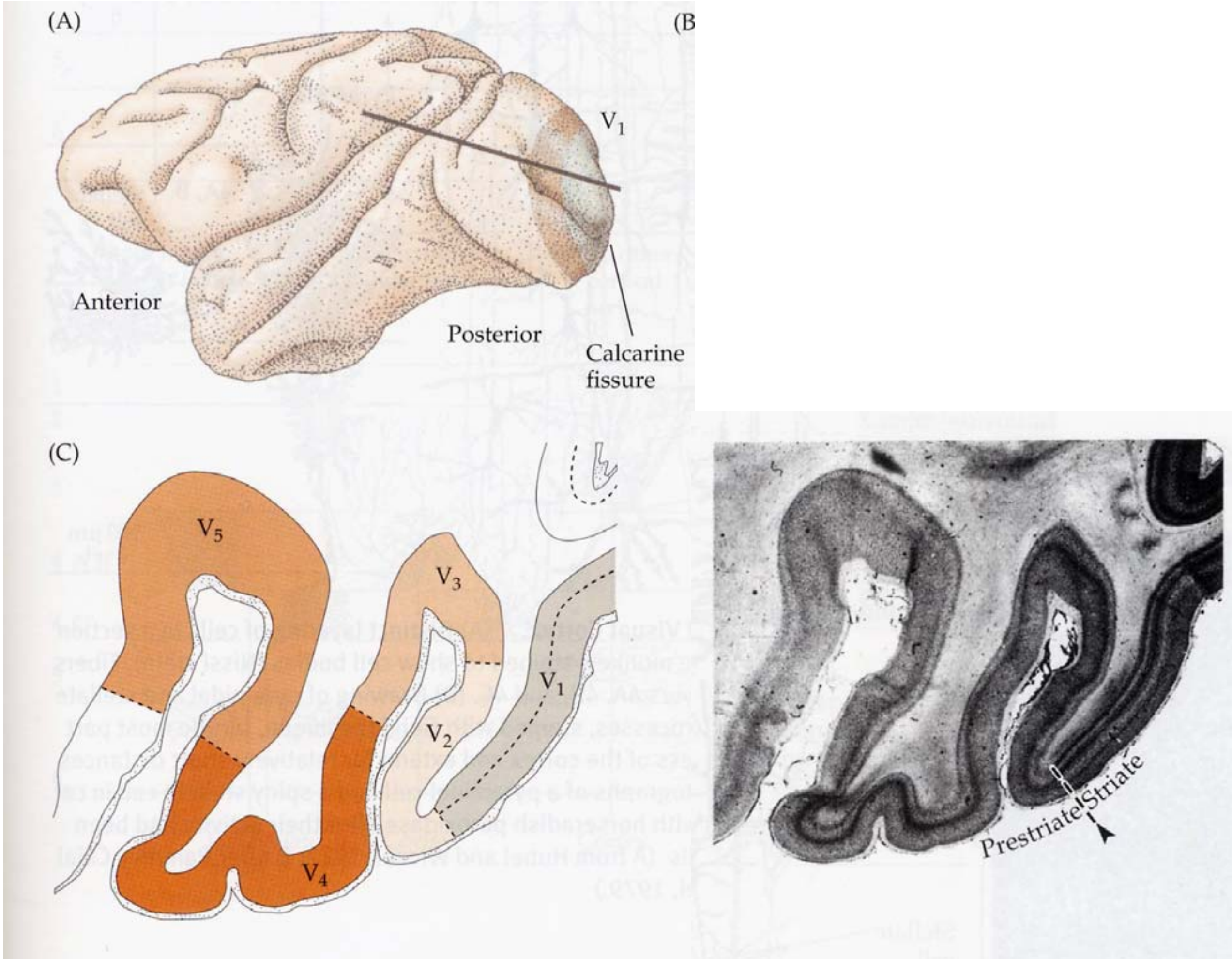


Angelucci et al, 2002

Given the extent of the visual space over which the illusory effect occurs it is almost certain that **feedback connections** from extrastriate areas of visual cortex to V1 are involved



Chavane et al, J Physiol Paris, 2000

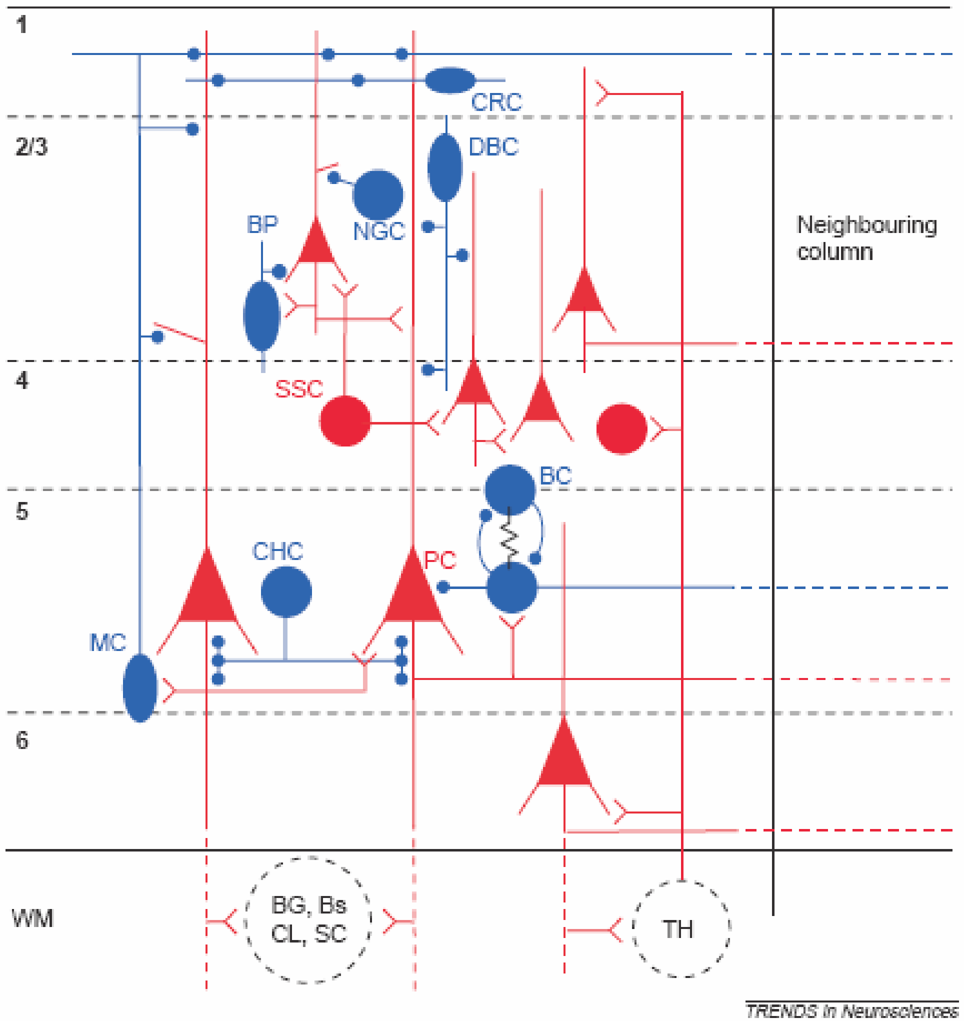


Fast-conducting axons connecting V1 to the other visual cortical areas are carried in the “white matter”, a layer below layer 6 in the neocortex which has few if any neurons.

Feedforward and feedback connections project from and to different layers in the six-layered architecture of the visual cortex (and all neocortex)

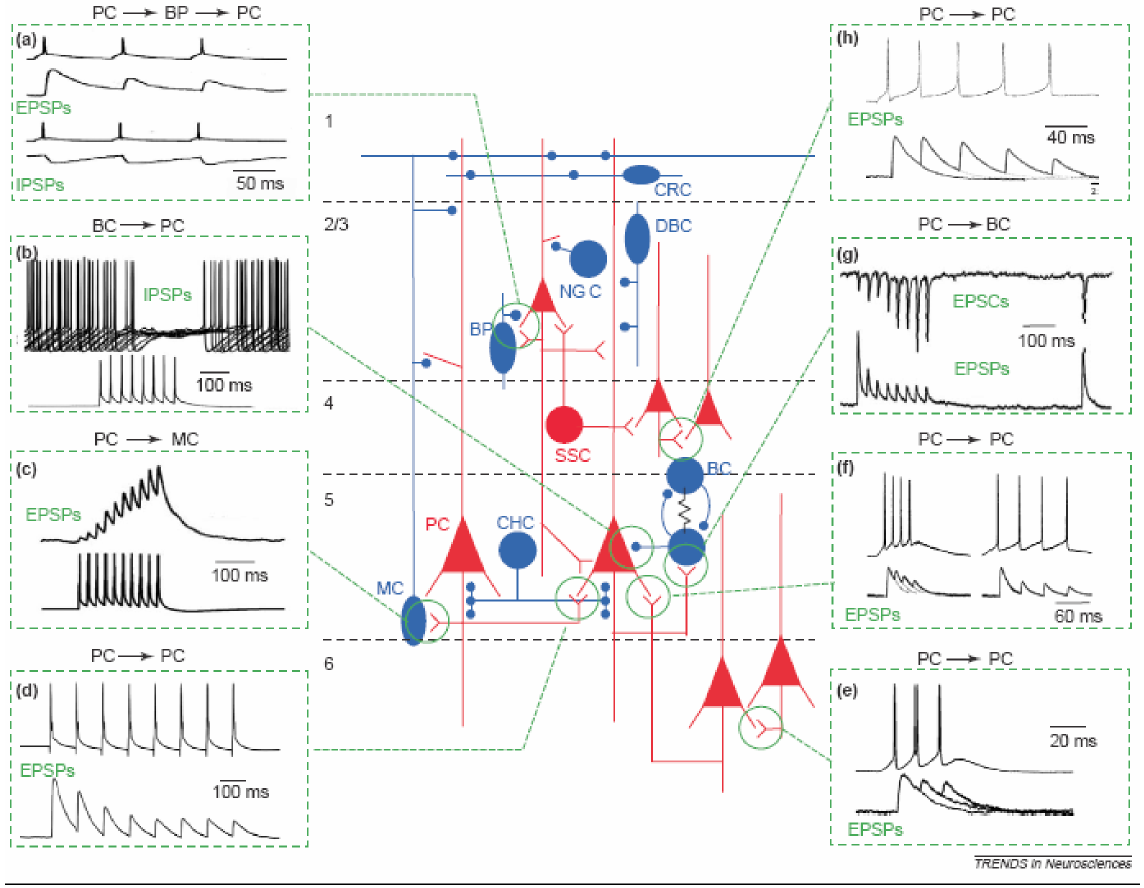
This leads us to a need to investigate the role of the different layers of this stereotypic neocortical architecture

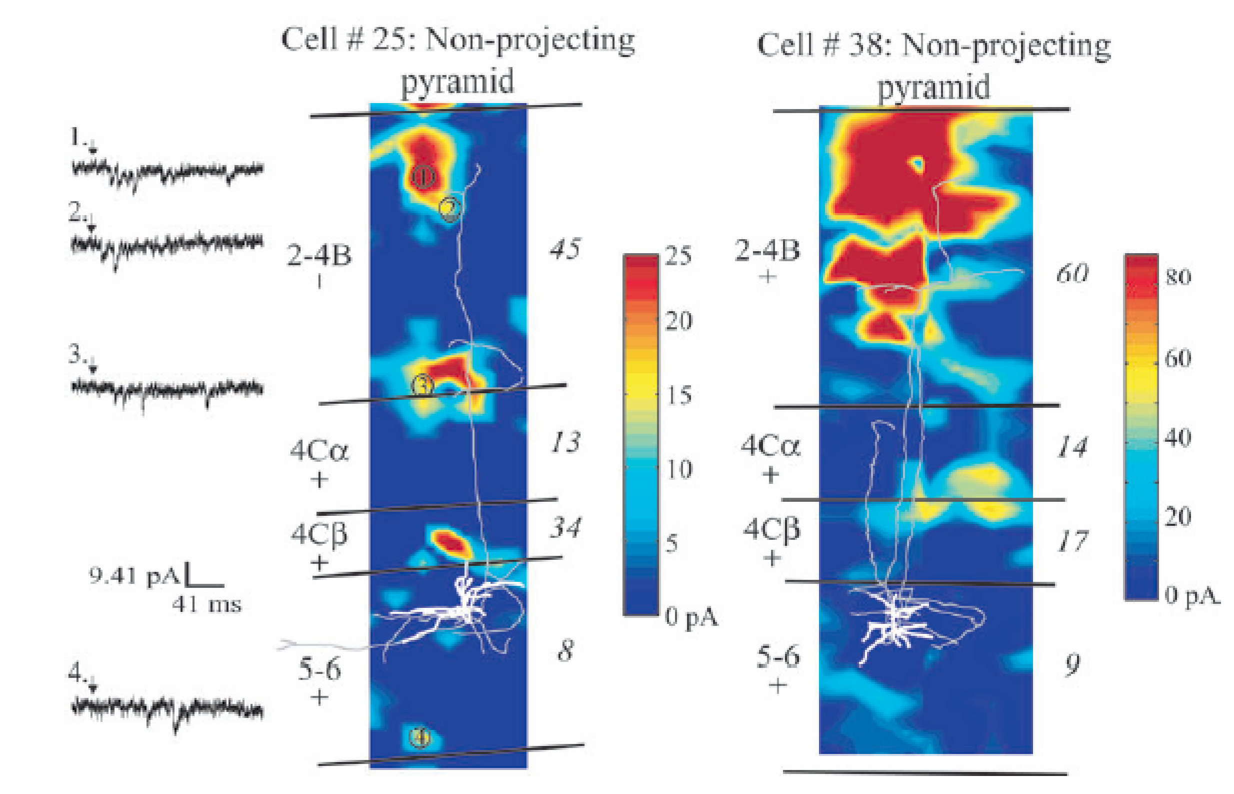
The neocortical laminar microcircuitry is characterised by a diversity of neuronal types and stereotypical intra- and interlaminar connectivity …



Grillner et al, TINS, 2005

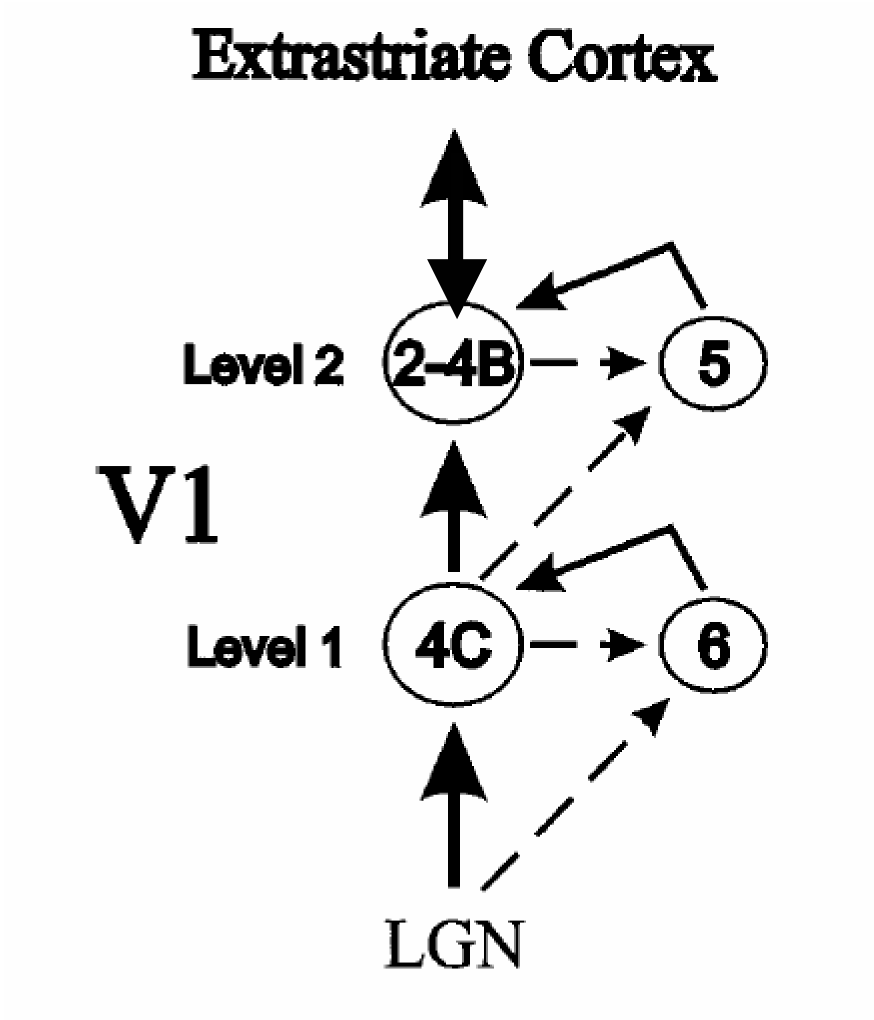
…and by a diversity of synaptic and neuron response dynamics …





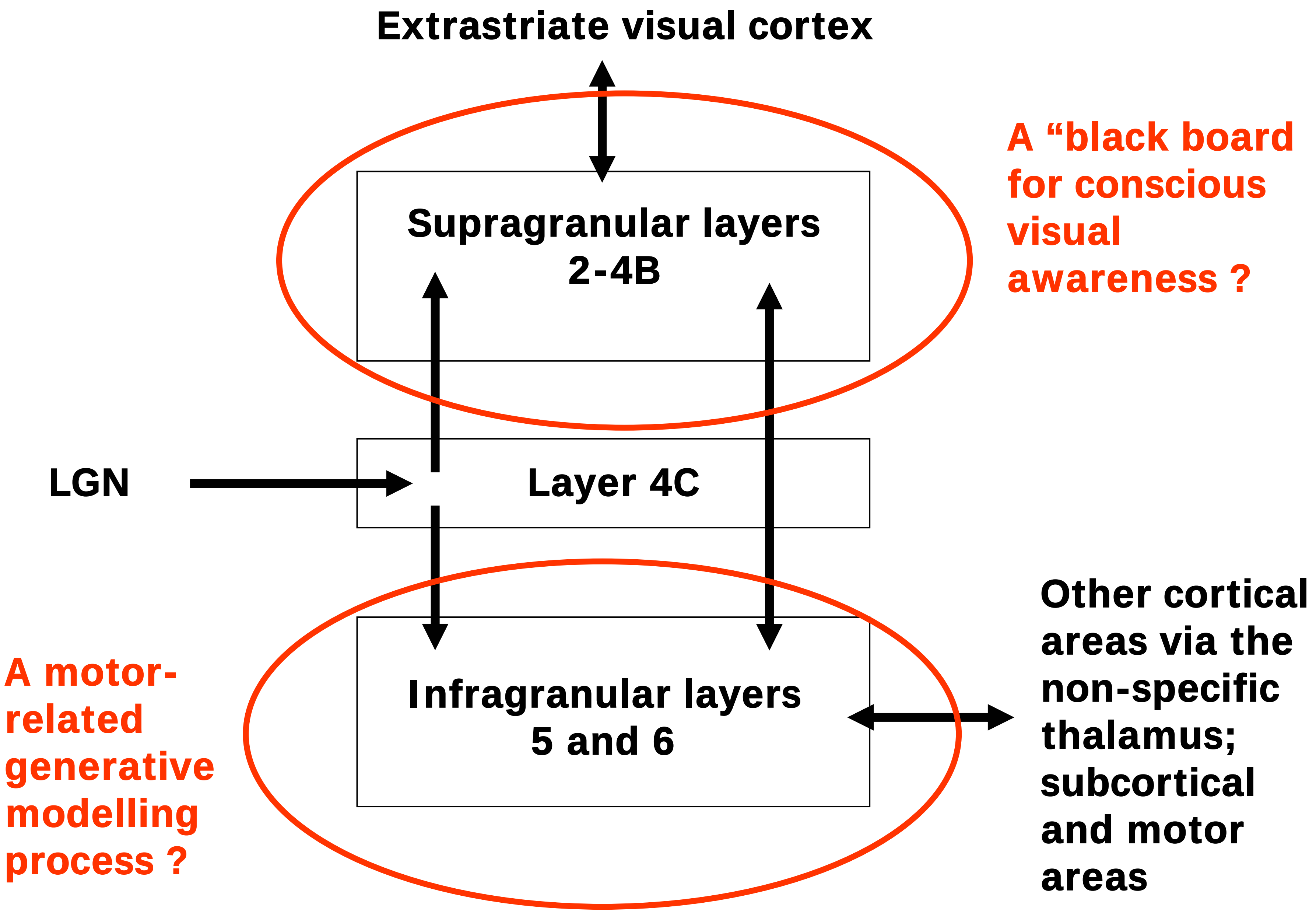
Briggs and Callaway, 2005

Laminar patterns of local excitatory input to neurons in each layer can be observed using scanning laser photostimulation combined with intracellular dye injection, eg for the layer 5 pyramidal neurons in macaque V1 shown above



Callaway, Ann Rev Neurosci, 1998

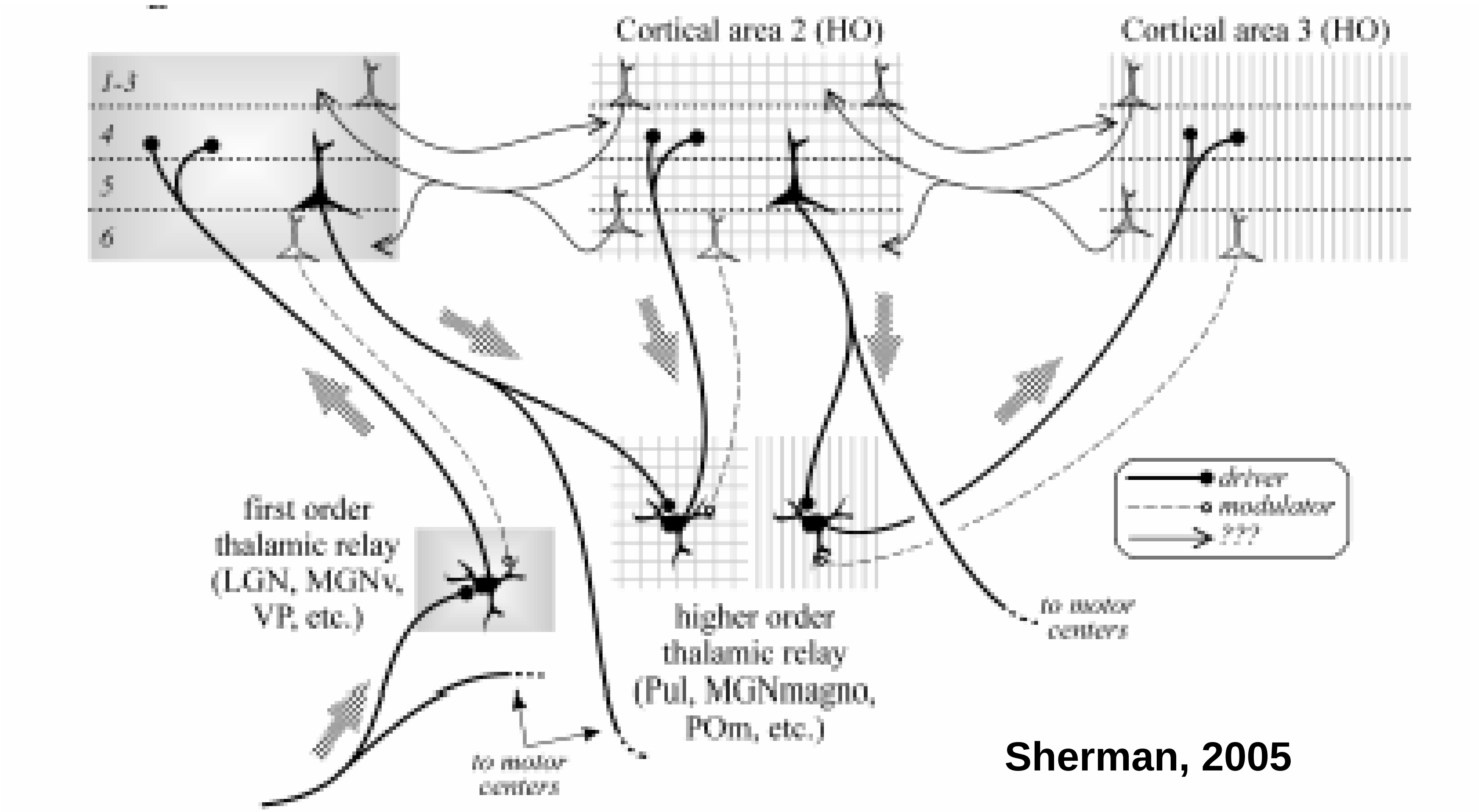
By considering the relative strengths of the intralaminar connections and making inferences about which are feedforward versus feedback, it is possible to construct simplified local circuit models, such as this two-level model proposed by Callaway (1998) which suggests distinctive feedback roles for layers 5 and 6


Extrastriate visual cortex
Supragranular layers
2-4B
A "black board for conscious visual awareness ?
LGN
Layer 4C
Infragranular layers
5 and 6
A motor-related generative modelling process ?
Other cortical areas via the non-specific thalamus; subcortical and motor areas

What is the role of cortical circuitry in conscious visual awareness?

- The visual pathways have both **feedforward** connections (from the retina to temporal and parietal cortical areas) and massive **feedback** connections (from higher order areas to V1 and from V1 to LGN)

- Recent experiments indicate that cortical areas V1 and V2 may behave as **“active blackboards”** that integrate the results of computations performed in higher order visual and motor areas (Bullier, 2001)

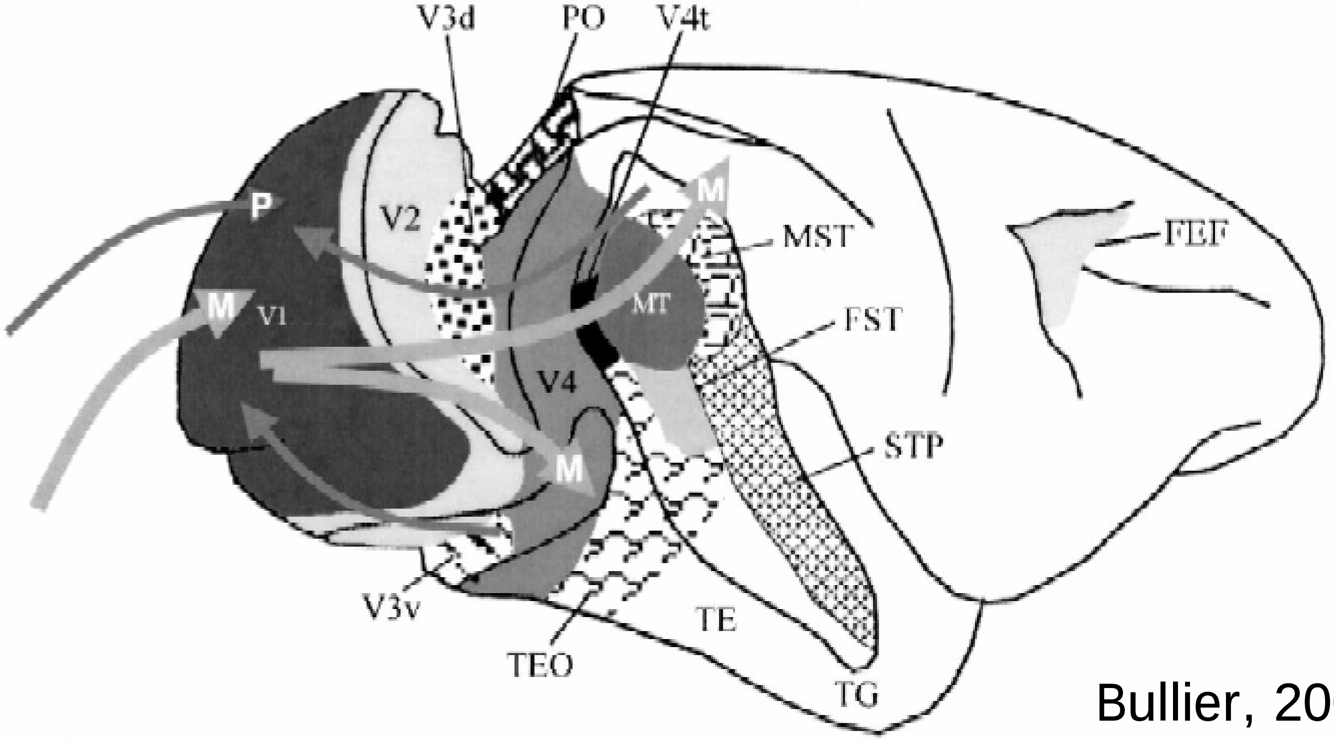


Sherman, 2005

A multilevel hierarchy of generative model processes?

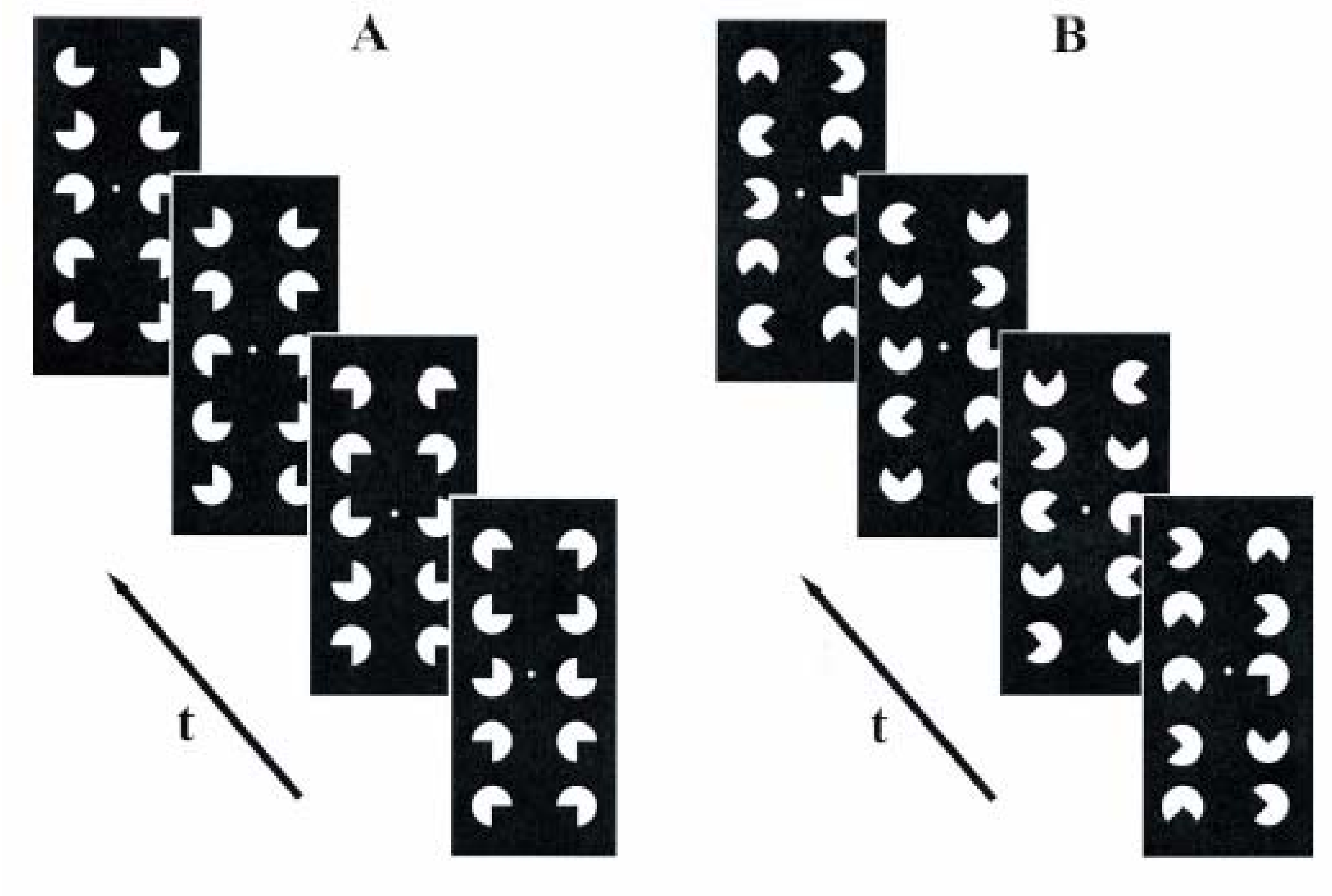
The shortest latencies of activation do not simply correspond to the lowest order areas in the visual hierarchy, eg MT, MST and FEF receive visual input well before the parvocellular pathway in V1

Bullier, 2001



Bullier, 2001

Fast conducting M pathways can activate areas MT, MST and FEF fast enough to allow them to send activation back to V1 and V2 in time for the arrival of the visual information in the P pathway



The perception of the illusory moving rectangle elicits a strong response in both MT and V1

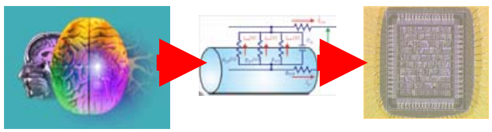
Bullier, 2001

Summary

- A knowledge and understanding of the nature and operation of the architecture and circuitry of the brain, in particular the neocortex, is important to a full understanding of cognition
- In particular cortical circuitry underlies the way in which local perceptual brain processes is mapped into global perceptual awareness
- Visual hallucinations and illusions can help us to understand the nature of the cortical architecture and processes which result in visual perception
- The powerful feedback connectivity in the visual pathways is important in understanding the way in which conscious visual awareness might result from the spatiotemporal interactions between primary and higher order visual cortical areas

A Novel Computing Architecture for Cognitive Systems based on the Laminar Microcircuitry of the Neocortex

The COLAMN Project



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School of Computer Science, Manchester University	*Prof Steve Furber*
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5	Albert-Ludwigs-Universität Freiburg	ALUF
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7	Technische Universität Graz	TUG
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