

Physiology of vision

- Light enters through the **lens** of the eye
- Image is **inverted & focused** to be projected on the **retina**, which is composed of **photoreceptors**. Photoreceptors translate external light stimuli into neural signals through 2 types of **photopigments**
 - **Rods** are sensitive to low level of stimulation -> most useful at night
 - Distributed throughout entire retina
 - **Cones** (3 types) require more intense levels of light, but can recognise colours
 - Densely packed near **fovea** (centre of retina) & few cones in the peripheral regions of the retina
- **Ganglion cells** are the output neurons from the retina, receiving input from rods/cones via bipolar cells. Their axons form the **optic nerve** that transmit visual information to the CNS
 - Ganglion cells have different receptive fields: more than one or a single photoreceptor can project to a single neuron
 - Convergence: many neurons project to a single neuron
 - The **retinogeniculate pathway** contains 90% of the axons in the optic nerve & provides input to the cortex via the **geniculocalcaral pathway**, which begins in the **LGN** & terminates in the **primary visual cortex V1** of the occipital lobe.
 - Until here the visual information has been processed by at least 4 neuron types: photoreceptors, bipolar cells, ganglion cells & LGN cells
 - The remaining 10% of optic fibres innervate **subcortical areas** (pulvinar nucleus of thalamus + superior colliculus)
- **Receptive field** = place in outside world in which stimulus must be presented in order to activate a single neuron in the brain

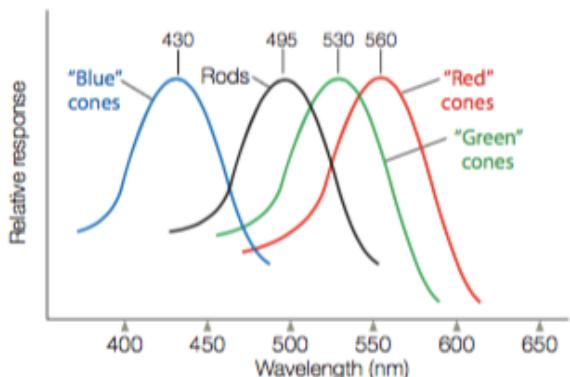


FIGURE 5.22 Spectral sensitivity functions for rods and the three types of cones.

The short-wavelength ("blue") cones are maximally responsive to light with a wavelength of 430 nm. The peak sensitivities of the medium-wavelength ("green") and long-wavelength ("red") cones are shifted to longer wavelengths. White light, such as daylight, activates all three receptors because it contains all wavelengths.

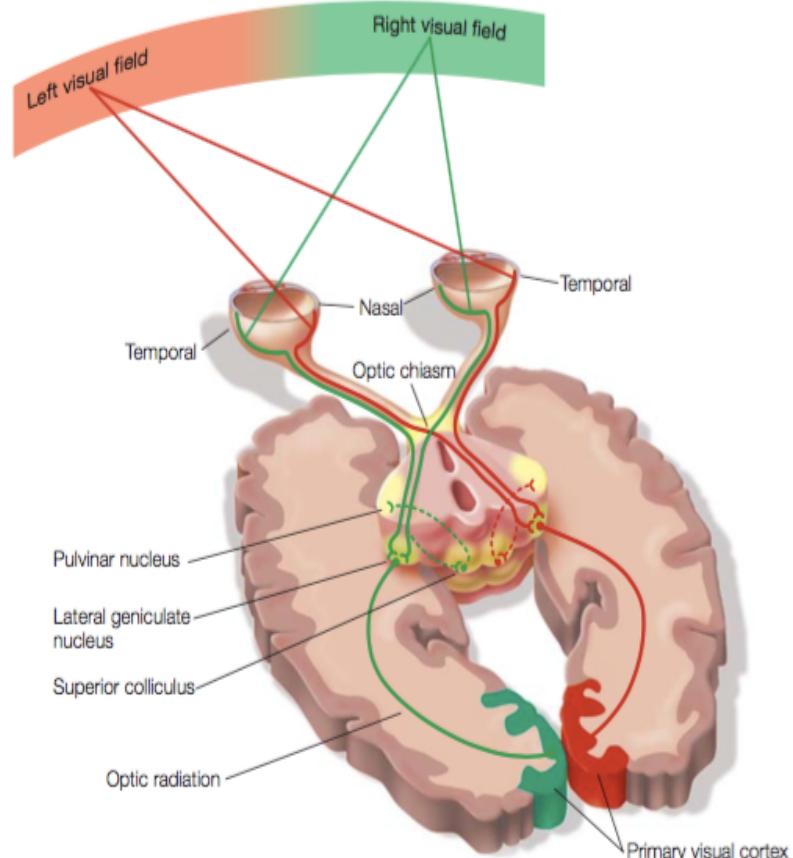


FIGURE 5.23 The primary projection pathways of the visual system.

The optic fibers from the temporal half of the retina project ipsilaterally, and the nasal fibers cross over at the optic chiasm. In this way, the input from each visual field is projected to the primary visual cortex in the contralateral hemisphere after the fibers synapse in the lateral geniculate nucleus (geniculocalcaral pathway). A small percentage of visual fibers of the optic nerve terminate in the superior colliculus and pulvinar nucleus.

More convergence → bigger receptive field

Each receptor has a receptive field

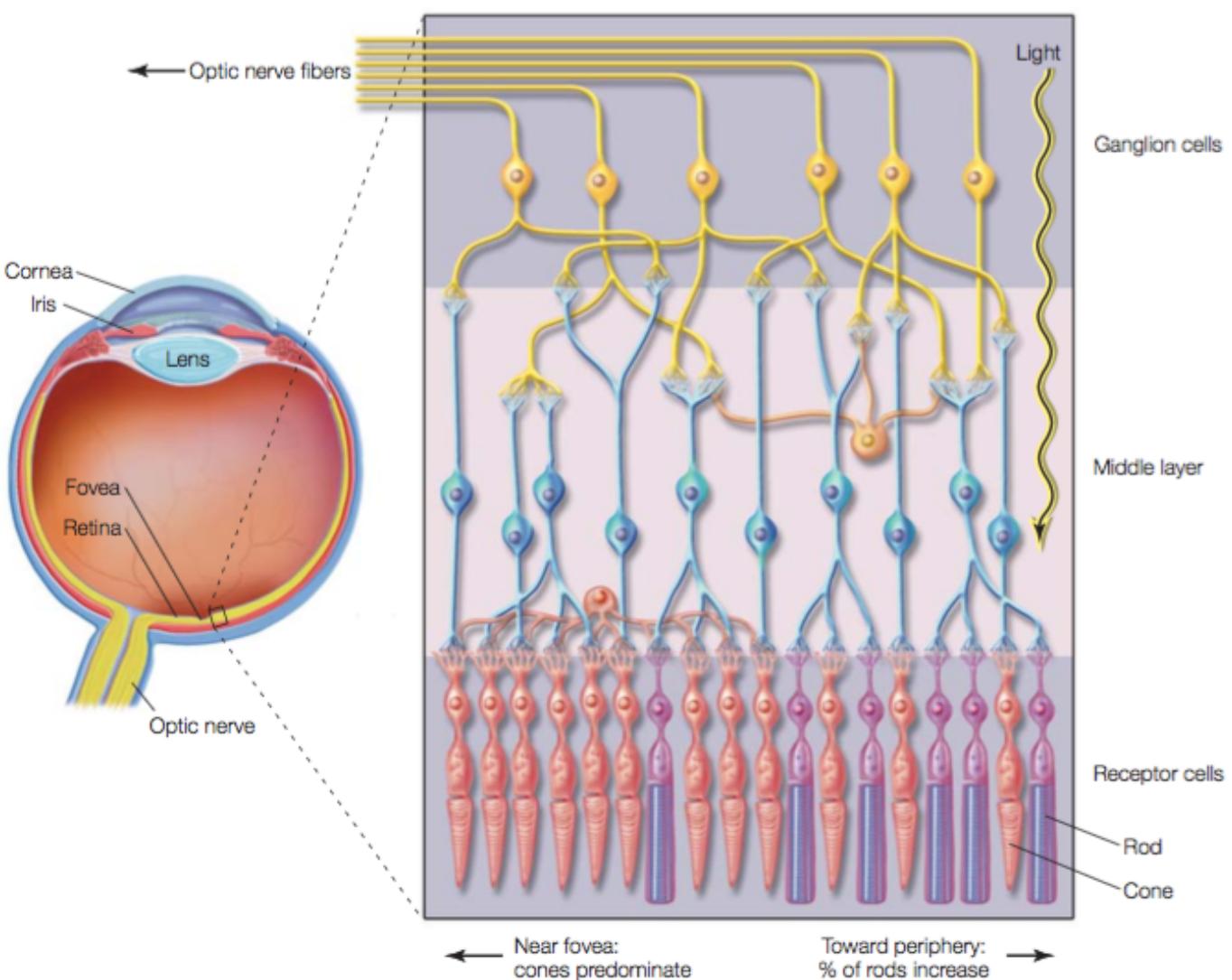
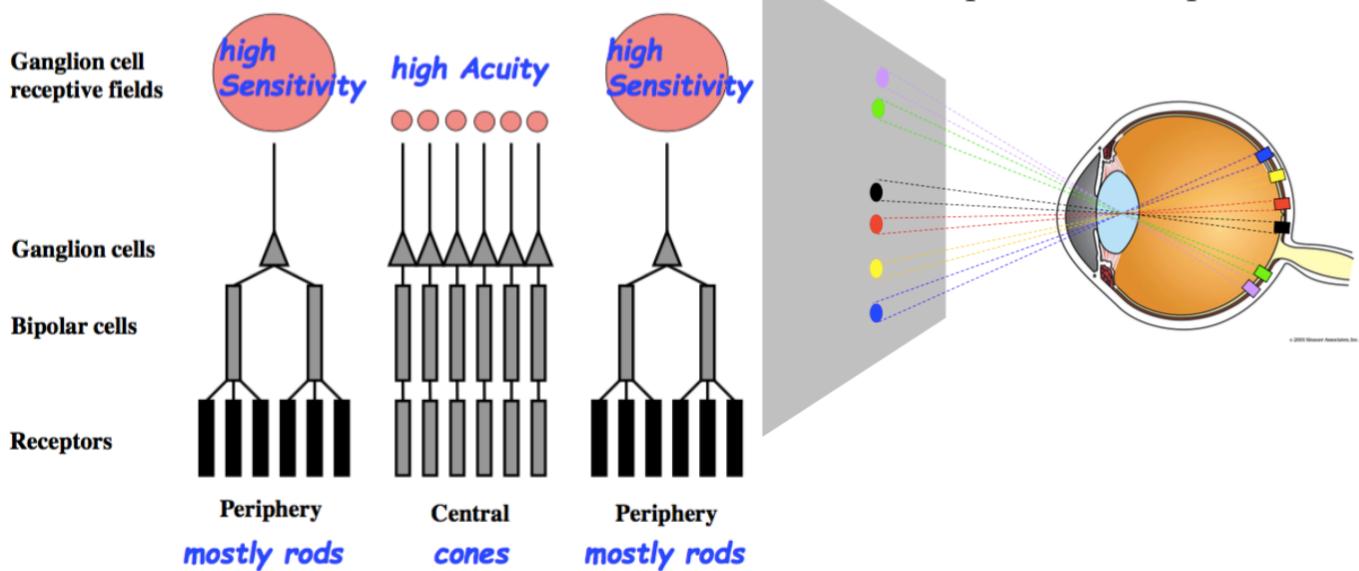


FIGURE 5.21 Anatomy of the eye and retina.

Light enters through the cornea and activates the receptor cells of the retina located along the rear surface. There are two types of receptor cells: rods and cones. The output of the receptor cells is processed in the middle layer of the retina and then relayed to the central nervous system via the optic nerve, the axons of the ganglion cells.

Cortical visual areas

- Topographic representation theory:
Each visual area of cortex has a topographic representation of external space in the contralateral hemifield.
Areas close in the hemifield are represented by neurons, close in space = **retinotopic map**. The direct link between neural activity & space is lost, but neurons in visual system represent space

- Boundaries between visual areas are marked by topographic discontinuities
- No specific hierarchical order connects visual areas, but extensive

patterns of convergence and divergence results in multiple pathways of topographic projection

- Alternative: specialisation theory holding that neurons within an area not only code where an object is located in the visual space, but also provide information about the object's attributes
 - > Processing is distributed among specialised areas, which each provides unique fraction of analysis

- Specialised areas defined by their retinotopic maps

- V1

- Neurons here are highly responsive to edges with a specific orientation

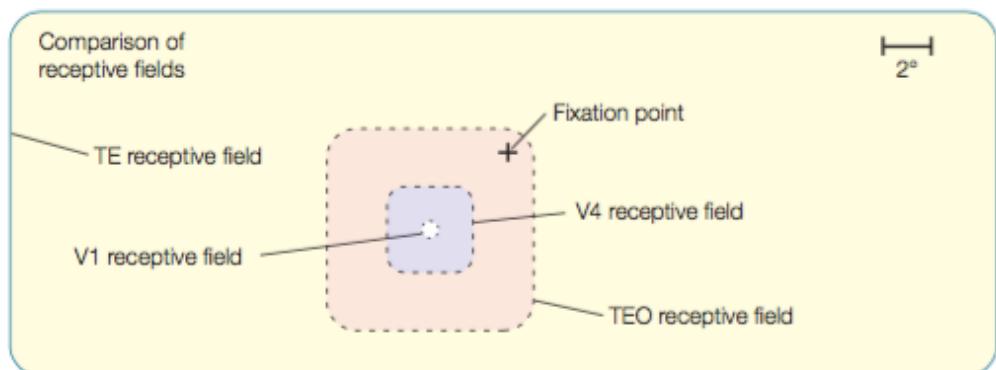
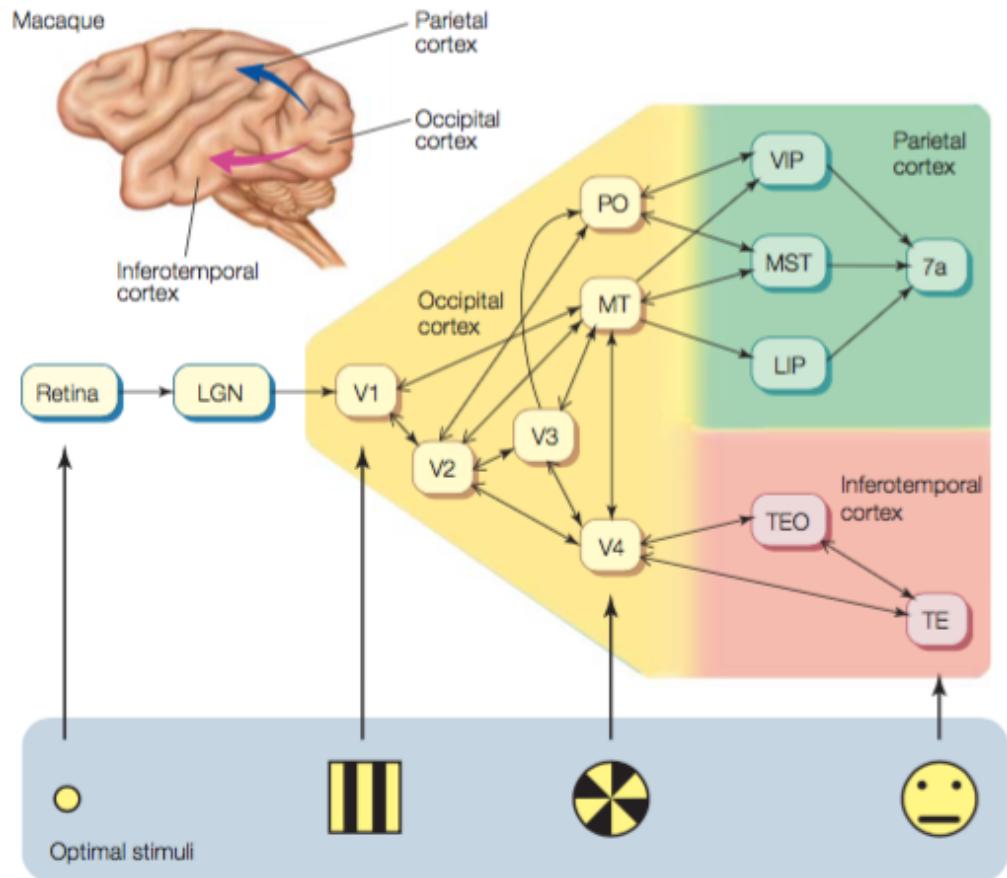


FIGURE 5.24 Prominent cortical visual areas and the pattern of connectivity in the macaque brain. Whereas all cortical processing begins in V1, the projections form two major processing streams, one along a dorsal pathway and the other along a ventral pathway (see Chapter 6). The stimulus required to produce optimal activation of a cell becomes more complex along the ventral stream. In addition, the size of the receptive fields increases, ranging from the 0.5° span of a V1 cell to the 40° span of a cell in area TE. The labels for the areas reflect a combination of physiological (e.g., V1) and anatomical (e.g., LIP) terms.

- Ganglion cells are responsive to circular field, while cortical neurons are responsive to edges.
- Orientation selectivity is the hallmark of neurons in V1
- Retinotopic organization of information
- The fovea is represented by greater amount of neurons than other retinal areas -> bigger patch of cortex processes input from fovea, due to its large number of photoreceptors -> bigger convergence.
 - Many neurons in a patch of 2mm by 2mm are centered on the same region in space. Within this space neurons vary in terms of preferred orientation and they alternate between columns that are responsive to either left eye or right eye input
 - Ocular dominance column = areas in which neurons have similar retinotopic tuning -> respond/show preference to input from left or right eye
- V2 & V3
 - Retinotopic organisation
- V4: involved in color foci, but is not color area (too simplistic) -> part of secondary visual areas, devoted to shape perception, as color can provide important cue about an object's shape
- V5: involved in motion = speed & direction

- Visual illusion studies show that perception is strongly dependent on higher visual areas, not activity in primary visual cortex

- Method: picture moving in a circle within visual field during fMRI -> regions activated when picture is in specific region in space shows which brain area processes specific area in space.

LGN

- 6 Layers
 - ipsi- 2,3,5, contralateral 1,4,6;
 - magno 1,2; parvo 3,4,5,6
- Retinotopy
- Characteristics of ganglion-cells that provide input to LGN:
 - M-cells (large cell bodies, fires in bursts, movement)
 - P-cells (small cell bodies, sustained firing, color, texture, patterns, depth)
 - (K-cells)

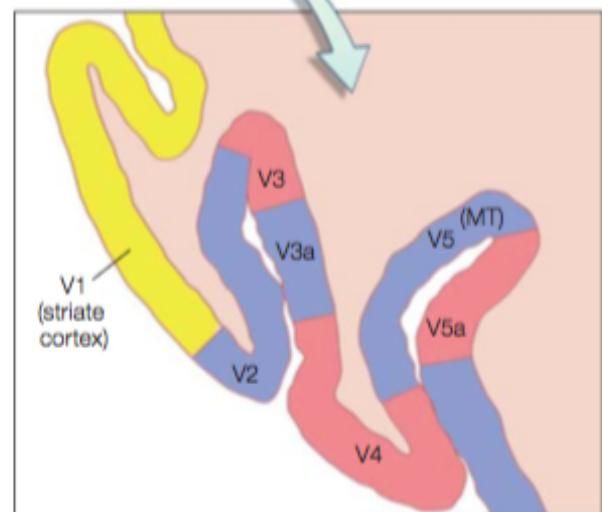
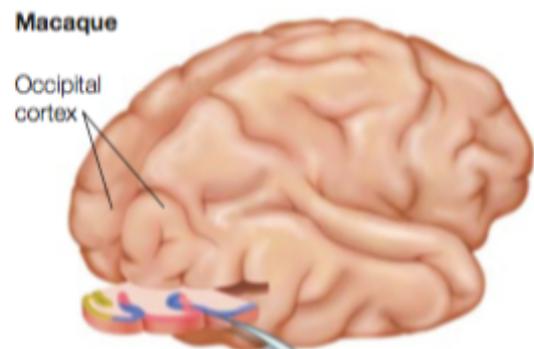
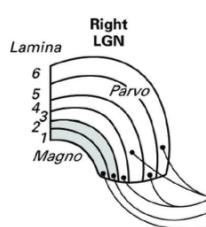
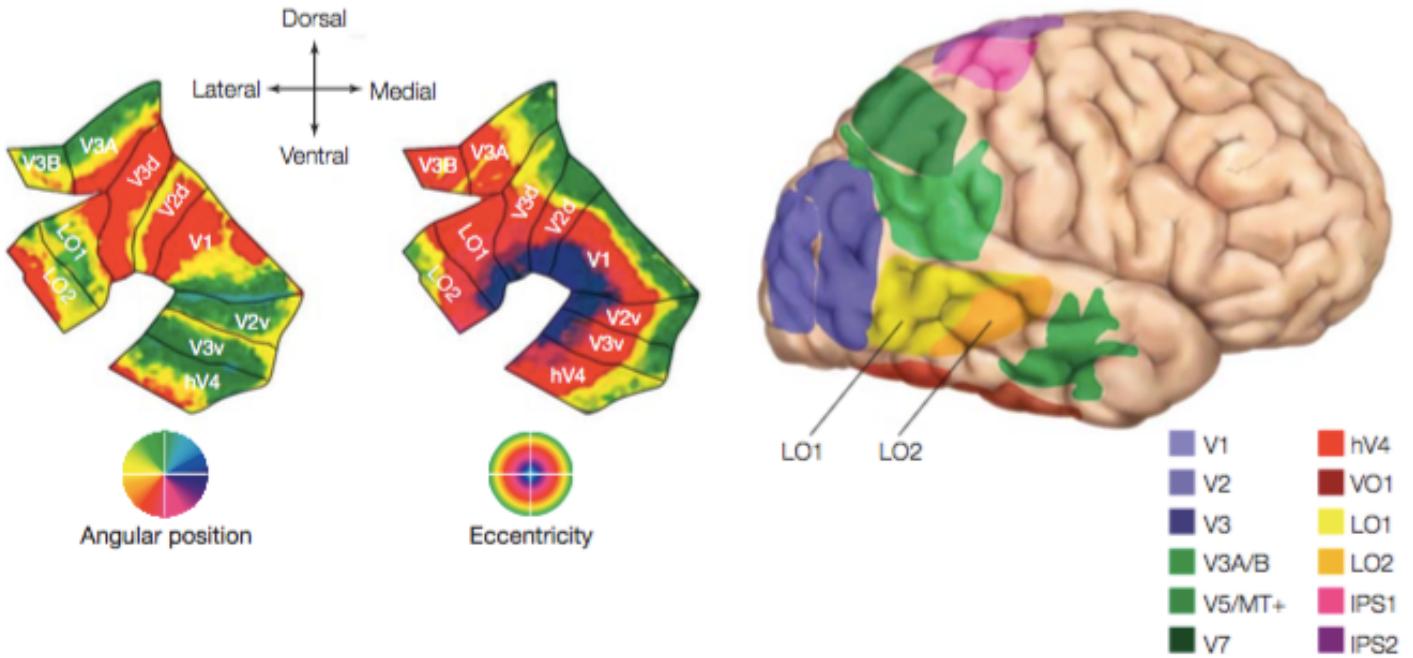


FIGURE 5.25 The boundaries between adjacent visual areas have topographic discontinuities.

An area is defined by a discontinuity or reversal in the retinotopic representation. Along the continuous ribbon of cortex shown here, seven different visual areas can be identified. However, processing is not restricted to proceeding from one area to the next in a sequential order. For example, axons from V2 project to V3, V4, and V5/MT.



a

b

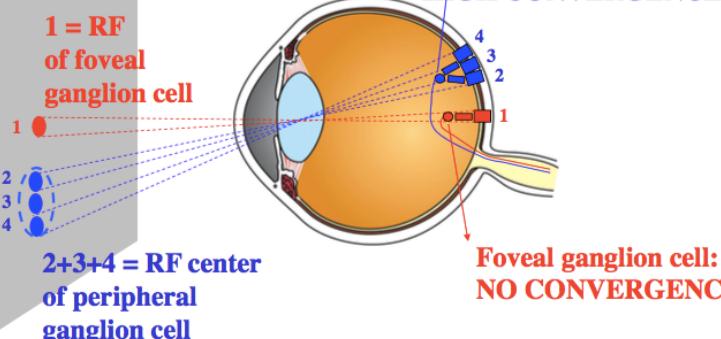
FIGURE 5.30 Two retinotopic areas in human lateral occipital cortex (LOC).

(a) The circular displays at the bottom represent the display on which a stimulus was projected, with the person instructed to fixate at the center of the crosshair. Across the scanning run, the position of the stimulus spans visual space. Left side shows color coding of activation patterns on flat map of visual cortex when the angular position of a stimulus was varied. For example, areas responding when the stimulus was presented below fixation are coded as red. Multiple retinotopic maps are evident in dorsal and ventral regions. Right side shows color coding of activation patterns when the eccentricity of the stimulus was varied (e.g., dark purple indicates activation areas when stimulus was at center of fixation).
 (b) Position of visual areas shown in (a) on an inflated brain. The size and location can only be approximated in a lateral view of the 3-d image.

Convergence = adding together of inputs

The amount of convergence
determines the size of the receptive
field (RF)

Peripheral ganglion cell:
HIGH CONVERGENCE



Convergence creates neurons with very large receptive fields that are sensitive to complex things

From analysis of light
by *circular* receptive fields...

to the analysis of image boundaries
by *oriented* receptive fields

To the analysis of complex
objects by large unoriented receptive fields

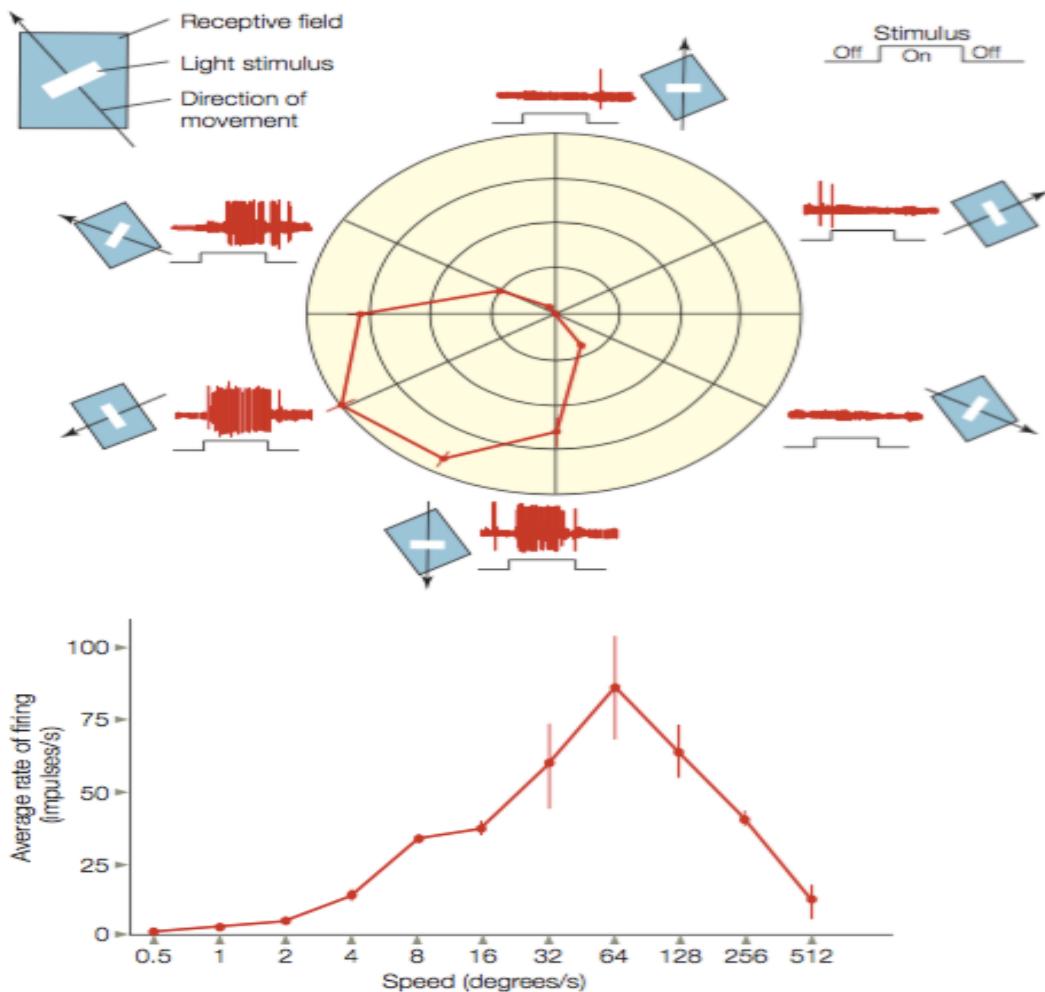
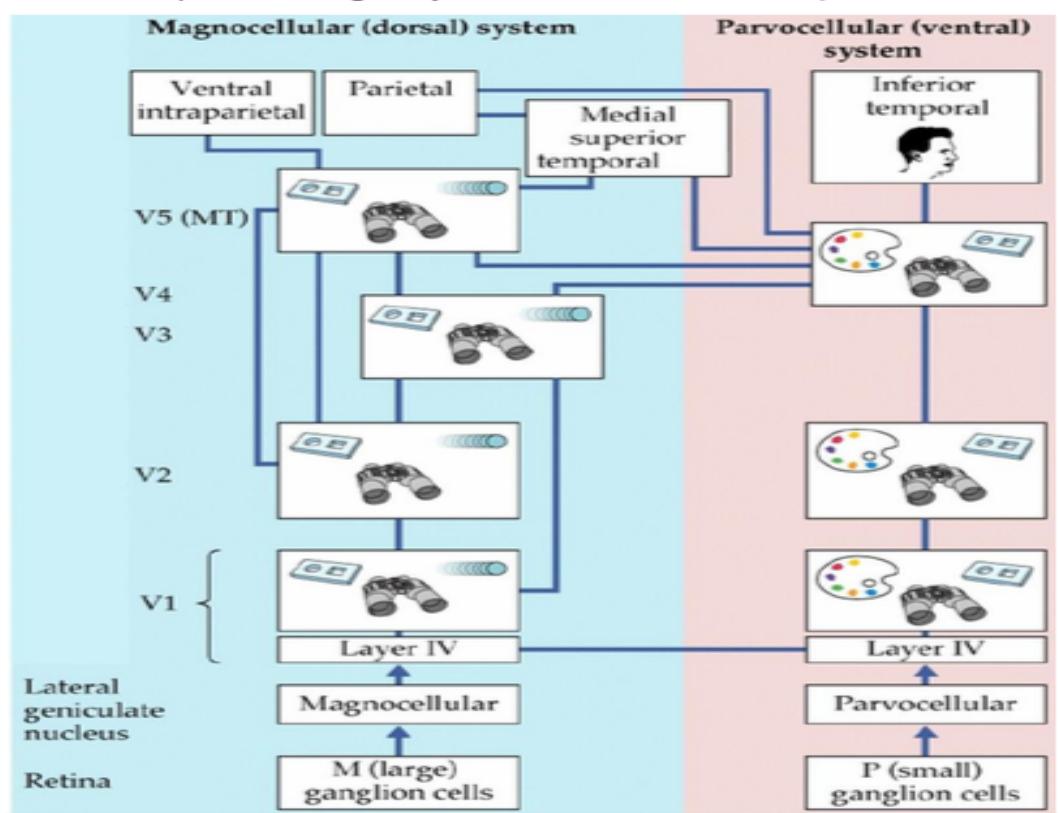


FIGURE 5.26 Direction and speed tuning of a neuron from area MT.

(a) A rectangle was moved through the receptive field of this cell in various directions. The red traces beside the stimulus cartoons indicate the responses of the cell to these stimuli. In the polar graph, the firing rates are plotted; the angular direction of each point indicates the stimulus direction, and the distance from the center indicates the firing rate as a percentage of the maximum firing rate. The polygon formed when the points are connected indicates that the cell was maximally responsive to stimuli moved down and to the left; the cell responded minimally when the stimulus moved in the opposite direction. **(b)** This graph shows speed tuning for a cell in MT. In all conditions, the motion was in the optimal direction. This cell responded most vigorously when the stimulus moved at 64°/s.



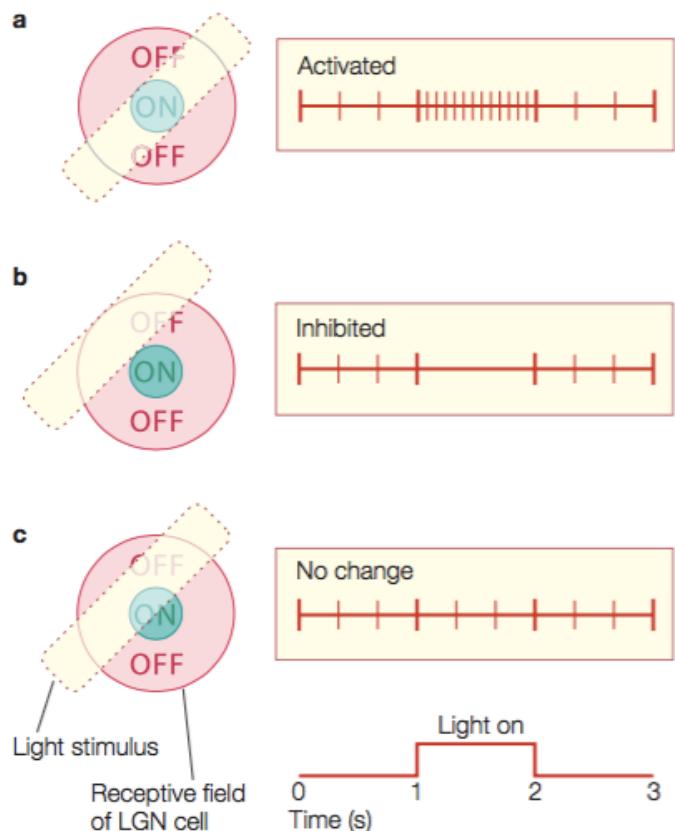


FIGURE 1 Characteristic response of a lateral geniculate nucleus (LGN) cell.

Cells in the LGN have concentric receptive fields with either an on-center, off-surround organization or an off-center, on-surround organization. The on-center, off-surround cell shown here fires rapidly when the light encompasses the center region (a) and is inhibited when the light is positioned over the surround (b). A stimulus that spans both the center and the surround produces little change in activity (c). Thus, LGN cells are ideal for signaling changes in illumination, such as those that arise from stimulus edges.

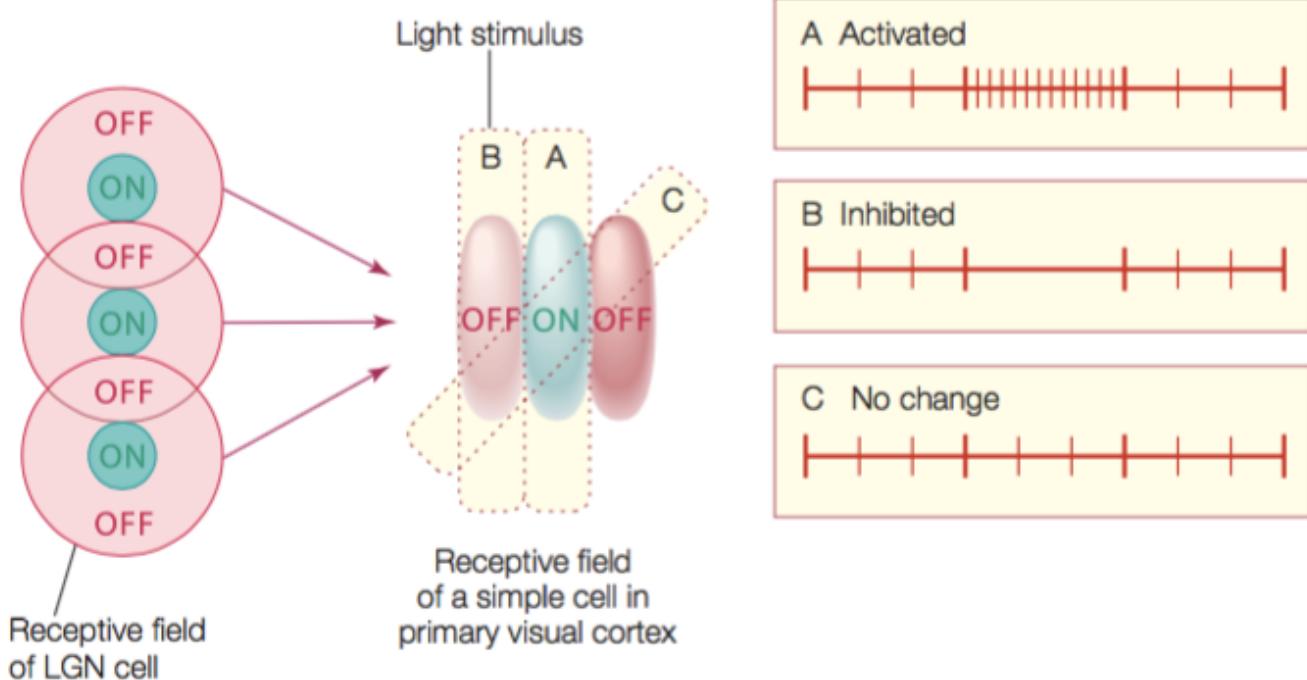
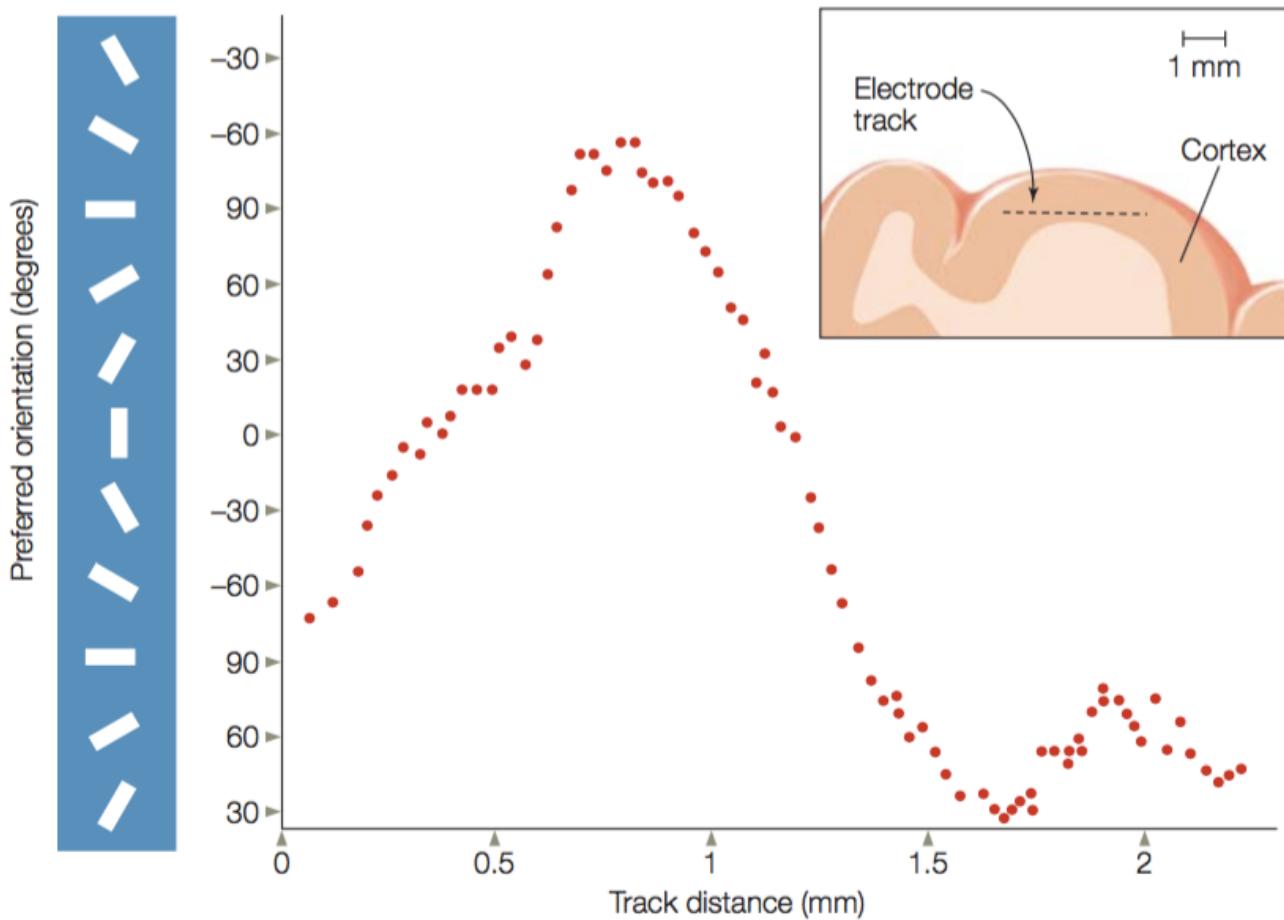
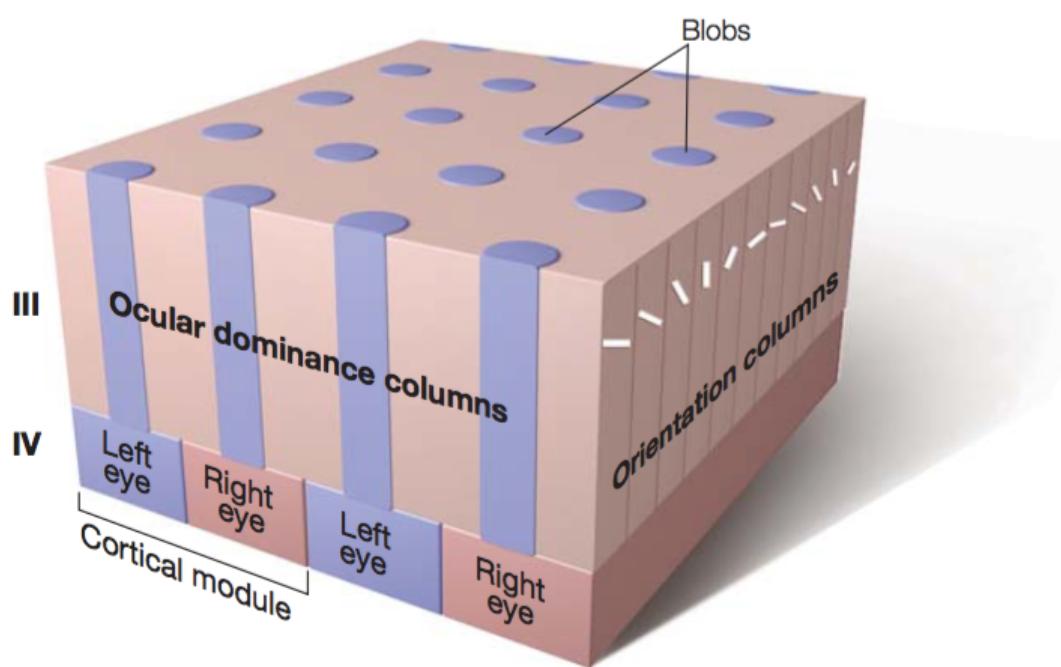


FIGURE 2 Simple cells in the primary visual cortex can be formed by the linking of outputs from concentric lateral geniculate nucleus (LGN) cells with adjacent receptive fields. In addition to signaling the presence of an edge, simple cells are selective for orientation. The simple cell illustrated here is either excited or inhibited by an edge that follows its preferred orientation. It shows no change in activity if the edge is at a perpendicular orientation.



a



b

FIGURE 3 Feature representation within the primary visual cortex.

(a) As the recording electrode is moved along the cortex, the preferred orientation of the cells continuously varies. The preferred orientation is plotted as a function of the location of the electrode. (b) The orientation columns are crossed with ocular dominance columns to form a cortical module. Within a module, the cells have similar receptive fields (location sensitivity), but they vary based on input source (left or right eye) and sensitivity to orientation, color, and size. For example, the so-called blobs contain cells that are sensitive to color and finer details in the visual input. This organization is repeated for each module.

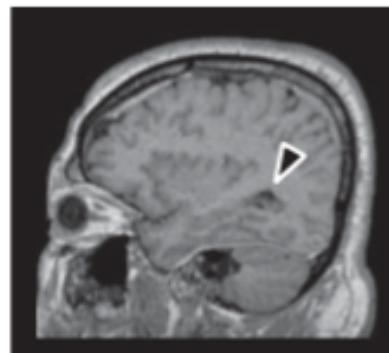
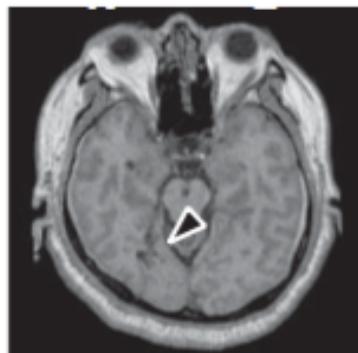
Deficits in visual perception

- **Acromatopsia** = deficits in color perception, often due to lesions encompassing V4 & neighbouring areas
 - **Dichromats** = people have only two different photopigments -> red-green or blue-yellow colourblind
 - **Anomalous trichromats** = people with all three photopigments, but one has abnormal sensitivity
 - **Achromatopsats** = people who see world without color, due to disturbances of CNS

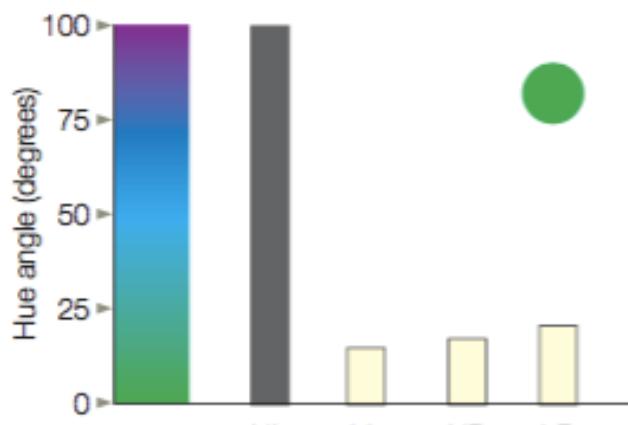
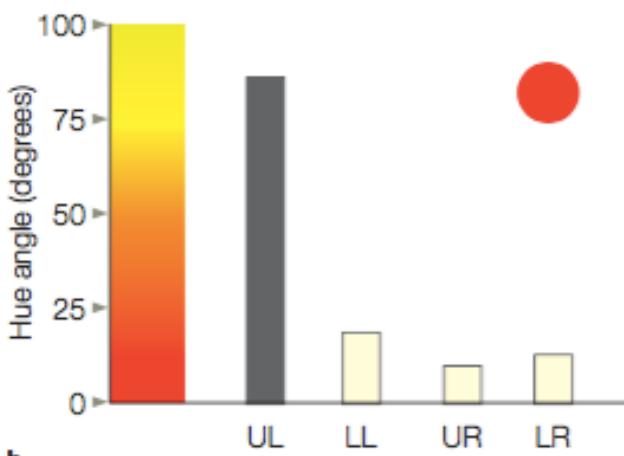


FIGURE 5.37 People with achromatopsia see the world as devoid of color.

Because color differences are usually correlated with brightness differences, the objects in a scene might be distinguishable and appear as different shades of gray. This figure shows how the world might look to a person with hemiachromatopsia. Most of the people who are affected have some residual color perception, although they cannot distinguish between subtle color variations.



a



b

FIGURE 5.38 Color and shape perception in a patient with a unilateral lesion of V4.

(a) MRI scans showing a small lesion encompassing V4 in the right hemisphere.

(b) Color perception thresholds in each visual quadrant. The patient was severely impaired on the hue-matching task when the test color was presented to the upper left visual field. The y-axis indicates the color required to detect a difference between a patch shown in each visual quadrant (UL = upper left, LL = lower left, UR = upper right, LR = lower right) and the target color shown at the fovea. The target color was red for the results shown in the top panel and green for the results shown in the bottom panel.

- **Akinetopsia** = deficits in motion perception, causing person to see objects appear in one space, then the next, instead of seeing things move continuously in space
 - TMS studies show important role of V5 in this deficit
 - Lesions involving temporoparietal cortices involving V5 & lateral & superior areas of V4
 - Severe degree of akinetopsia only in subjects with bilateral lesions

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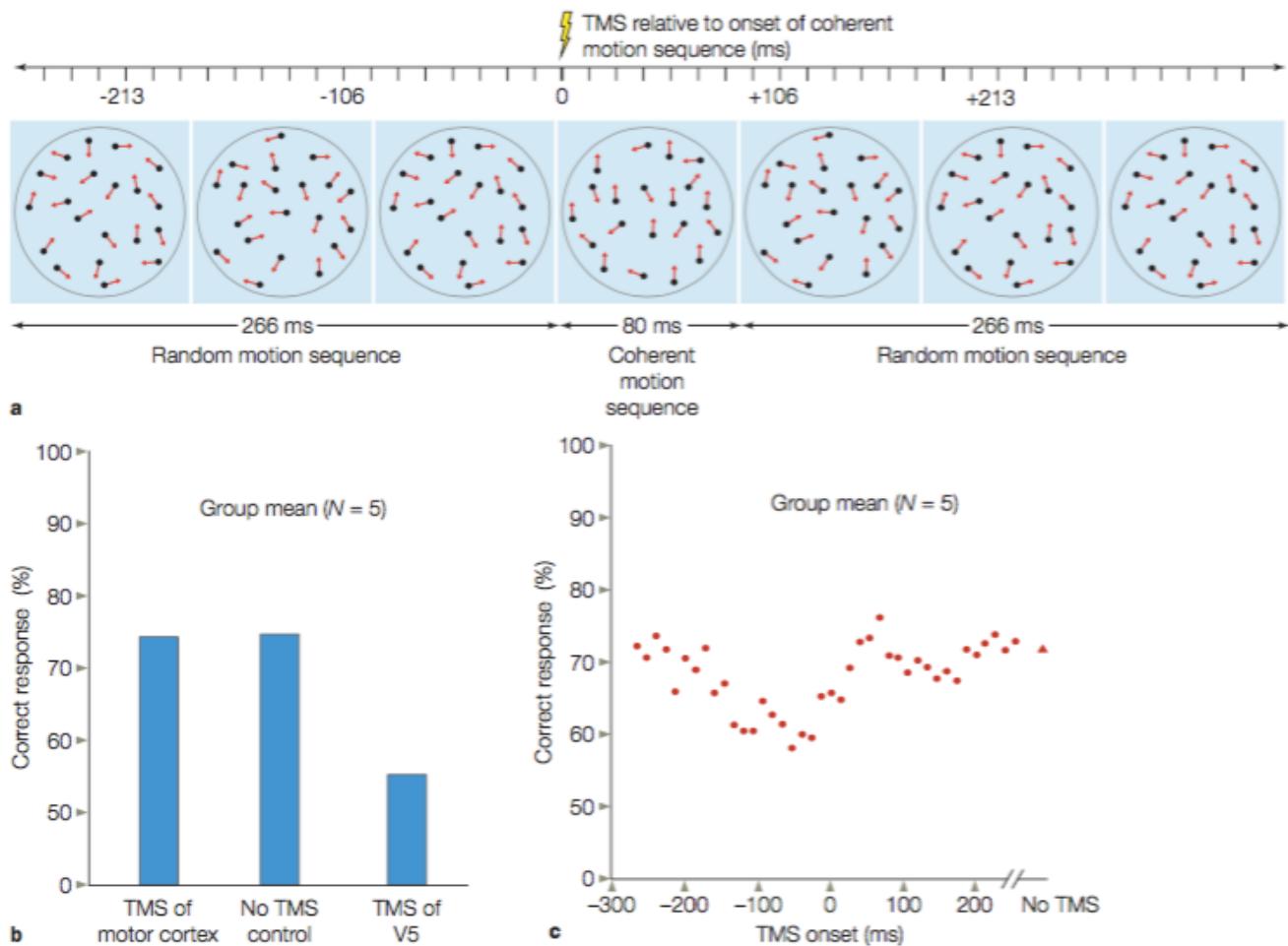


FIGURE 5.42 TMS over human V5 disrupts motion perception.

(a) The stimulus was an 80 ms display of moving dots in which a small percentage of the dots moved in the same direction. This display was preceded and followed by displays in which the direction of motion for all of the dots was random. (b) Performance was impaired when the TMS was applied over V5, relative to two control conditions (TMS over motor cortex or no TMS). (c) When the timing of the TMS pulse was varied to either come before the stimulus (negative values) or after the stimulus (positive values), two epochs of disruption were identified.

Perceptions without a visual cortex -> visual capabilities may persist without primary visual cortex, due to 10% contribution of subcortical visual pathways.

- **Hemianopia**: lesion in primary visual cortex, restricted to one half of the visual field, causing loss of perception, which is restricted to contralateral side of space.
 - Visual cortex lesion impart acuity, which is important for object identification
- **Scotomas**: discrete regions of blindness, caused by smaller lesions
 - **Patient D.P.**: Can he detect location of objects, presented within area of scotoma? Yes due to phenomenon of **blindsight** (not understood) = patient acts & feels as if he is blind, yet shows residual ability to localise stimuli presented in blind field

- **Agnosia:** failures in perception, despite intact visual processes of color, shape, motion analysis -> “failure of knowledge or recognition”
 - If disorder is limited to visual modality, the syndrome is called **visual agnosia**
 - -> Shows that object recognition is more than linking features to form a coherent whole, but depends on memories triggered by “the whole”

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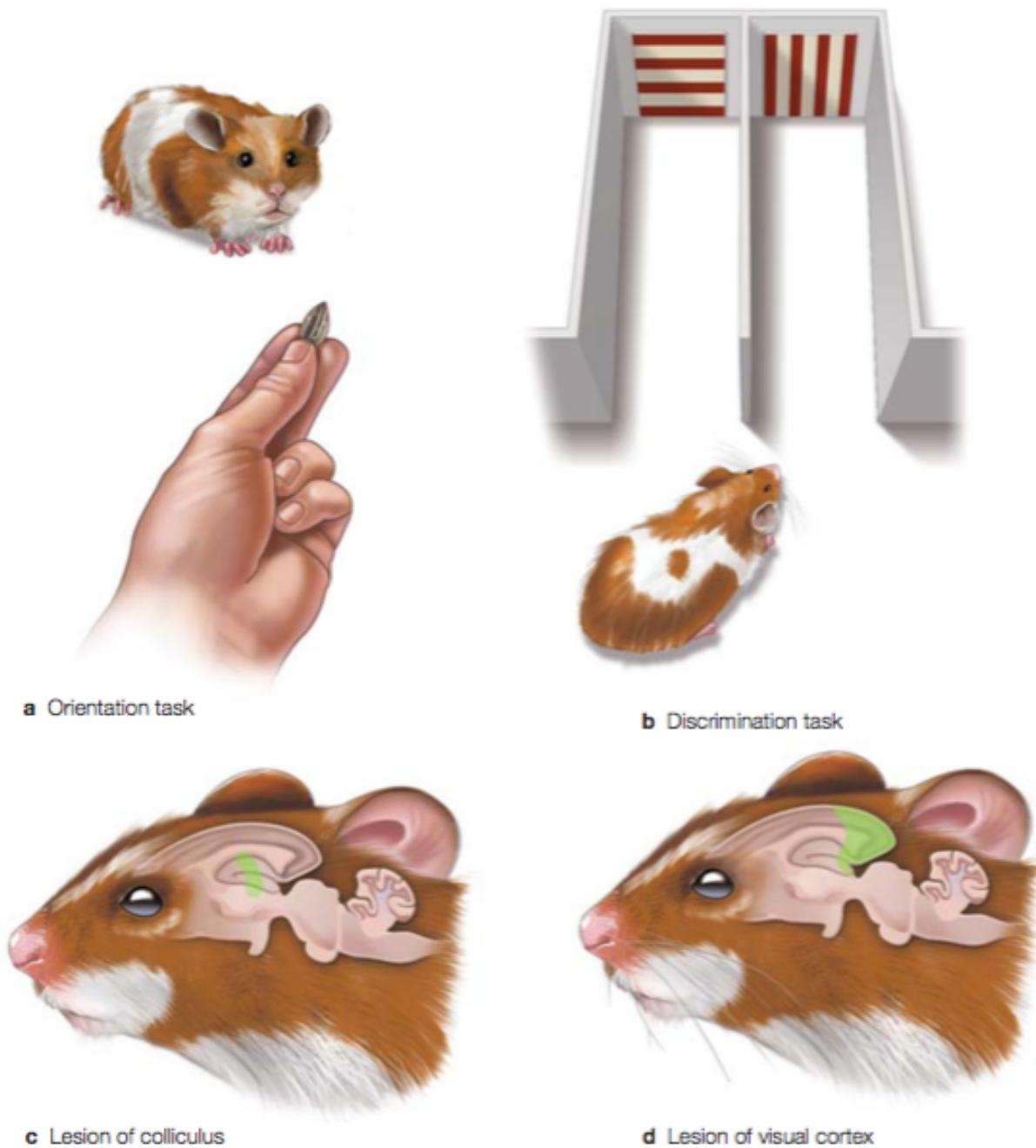


FIGURE 5.43 Double dissociation between lesions of the superior colliculus and visual cortex.
(a) In the orientation task, hamsters were trained to collect sunflower seeds that were held at various positions in space. **(b)** In the discrimination task, hamsters were trained to run down one of two alleys toward a door that had either horizontal or vertical stripes. **(c)** Lesions of the colliculus disrupted performance on the localization task. **(d)** Lesions of the visual cortex selectively impaired performance on the discrimination task.

Prosopagnosia = deficits in face perception, which cannot be attributed to deterioration in intellectual

function, but is specific to visual modalities -> patient's can recognise people based upon hearing voices

- Inverted face tasks: Only unaltered face recognition is impaired, NOT upside-down face recognition -> confirms special system for face recognition, which is more than linking its parts.
 - Bilateral or unilateral RH damage in occipital & temporal lobes
- **Acquired alexia** = reading problems after stroke/trauma, in which patient can understand & produce spoken speech, but has errors in visual domain of letter/word recognition
 - Like prosopagnosia it is within-category deficit -> failure to discriminate items that are much alike in appearance like misreading ball = doll
 - Different anatomy than prosopagnosia!
 - LH lesions of angular gyrus at junction of occipital, temporal & parietal lobes
 - Both alexia & prosopagnosia rarely occur in isolation -> most often entail some problems with object perception (agnosia) -> supports idea that object perception involves two independent processes

Perception of objects versus faces

- **Hypothesis:** Face recognition mechanisms are different from the ones of object recognition, rooted in evolutionary theory = facial recognition is of special importance & universal
- **Research:** two distinct regions of temporal lobe, preferentially activated in face recognition in animals:
Superior temporal sulcus & inferotemporal gyrus
 - In humans stronger activation in fusiform gyrus = **fusiform face area FFA**
 - Alternative: FFA not distinct to faces, but recruited when people have to make final perceptual discrimination among highly familiar stimuli
 - Face evoke much larger **N170** response during EEG, than for objects
 - **Face inversion effect:** recognition much harder if face is distorted or upside down, maybe due to inability to use specialised face-processing system, but must revert to analysis-by-parts mode
- **Pariahippocampal place area PPA:** engaged by stimuli containing information about spatial relations, or if people asked to classify objects according to some spatial property (indoor vs outdoor class of object)
 - Lesions -> people disoriented in new environments
- Distinction of processing
 - **Analytical processing** = analysis of structure & configuration of stimulus
 - Associated with LH
 - Most strongly associated with object perception
 - **Holistic processing**
 - Associated with RH
 - Most strongly associated with face perception

Cortical pathways for visual perception

- Primary sensory regions provide representations closely linked to physical properties, but perceptual experience more dependent on secondary regions
- Output from the occipital lobe runs through two major fibre bundles. In animal studies only bilateral lesions to the temporal or parietal lobe show deficits in distinguishing what or where, respectively.
 - **Inferior longitudinal fascicles**, creating the **ventral stream** -> specialised for **object perception & recognition**
 - Determines what we are looking at
 - Encompasses V1, V2, V3, V4, & located in temporal lobes, with specialised neurons
 - Receptive fields of neurons always encompass the fovea
 - Majority of neurons can be activated by a stimulus that falls within either the left or the right visual field
 - Neurons have diverse pattern of selectivity = 41% are activated by any stimulus, while 59% exhibit selectivity for stimuli
 - **Superior longitudinal fascicles**, creating the **dorsal stream** -> specialised for **spatial perception**
 - Determines where object is perceived & analyses spatial configuration between objects in a scene, which is crucial for interacting with an object
 - Encompasses V1, V2, V3, V5, located mostly in parietal lobes, with specialised neurons
 - Neurons can respond in non-selective manner
 - Responsiveness to stimuli that are presented in more eccentric parts of the visual field -> 40% have receptive fields close to the fovea, while 60% have receptive fields that exclude the foveal region -> ideal for detecting mere presence of stimuli
 - Critical to selective attention

Perception for identification versus perception for action

- Lesions to the parietal lobe produce severe disturbances in the ability to represent the world's spatial layout & spatial relations of objects in it.
 - The lesion often fall along the ventral pathway, especially in prosopagnosia patients, but frequently extend into parietal structures.
- **Agnosia patient D.F:** shows severe impairments in matching task, needing him to match the orientation of the card in his hand to that of the slot in a block, but no impairment in action task, during which he had to insert the card in the slot, which was done without hesitation
 - -> Processing systems make use of different sources of perceptual information = what and where systems support different aspects of condition
 - In blindsight information may be accessed by action systems, but not by conscious knowledge systems
- **Optic ataxia** patient, who often have lesions in parietal cortex, can recognise objects, yet cannot use visual information to guide their actions

- -> What-where or what-how dichotomy offers a functional account of two independent computational goals for higher visual processing

