

1. The brain: an overview

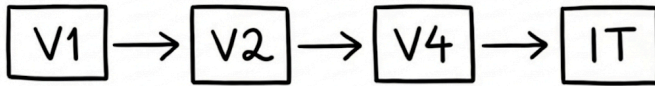
- **Hemispheres.** The brain is divided into two roughly symmetrical halves, connected by the corpus callosum.
 - **Left hemisphere:** biased towards language processing and analytical reasoning. Controls right side of the body.
 - **Right hemisphere:** biased towards spatial processing and face perception. Controls left side of the body.
- **Inner brain and outer brain.**
 - The outer shell of the brain is the cortex, an evolutionarily newer structure, distinctively enlarged in humans, responsible for higher-order cognition.
 - The inner brain includes structures that are evolutionarily older and involved in more basic functions.
- **Major subcortical structures.**
 - **Thalamus:** the central relay hub for nearly all sensory input (except olfaction) headed to the cortex.
 - **Hypothalamus:** regulates core survival functions: hunger, thirst, body temperature, circadian rhythms.
 - **Hippocampus:** critical for forming new declarative memories and for spatial navigation.
 - **Amygdala:** central role in processing emotions, especially fear.
 - **Basal ganglia:** a group of nuclei involved in voluntary movement, habit learning, and reward.
 - **Cerebellum:** rear base of the brain; motor coordination, balance, timing, motor learning.
 - **Brain stem and spinal cord.** The brain stem (midbrain, pons, medulla) connects the brain to the spinal cord. Controls breathing, heart rate, arousal, sleep-wake cycles. The spinal cord relays motor commands downward and sensory information upward.
- **Cortex.** The cerebral cortex is a thin sheet of neural tissue forming the outer surface of the brain. Extensively folded to maximize surface area.
 - **Grey matter:** the outer layer, where computation occurs; made up of neural cells bodies.
 - **White matter:** the underlying layer, wiring; made up of axons that connect cortex to cortex and below.

- **Lobes.** The cortex is divided into four lobes.
 - **Occipital lobe** (back): primary site of visual processing.
 - **Parietal lobe** (top): spatial awareness, sensory integration, attention.
 - **Temporal lobe** (side): auditory processing, language comprehension (left hemisphere), memory, object recognition.
 - **Frontal lobe** (front): the largest lobe; planning, decision-making, working memory, personality, motor control.
- **Notable functional areas.**
 - **Visual cortex:** areas in the occipital lobe (extending into temporal and parietal lobes) devoted to vision. V1 through V5 and higher areas.
 - **Motor cortex:** the rear part of the frontal lobe; topographic body map (motor homunculus); each region controls movement of a corresponding body part.
 - **Somatosensory cortex:** further back into the parietal lobe; forms a topographic body map (sensory homunculus).
 - **Prefrontal cortex:** forward part of front lobe; executive functions: planning, working memory, decision-making, impulse control, social behavior.

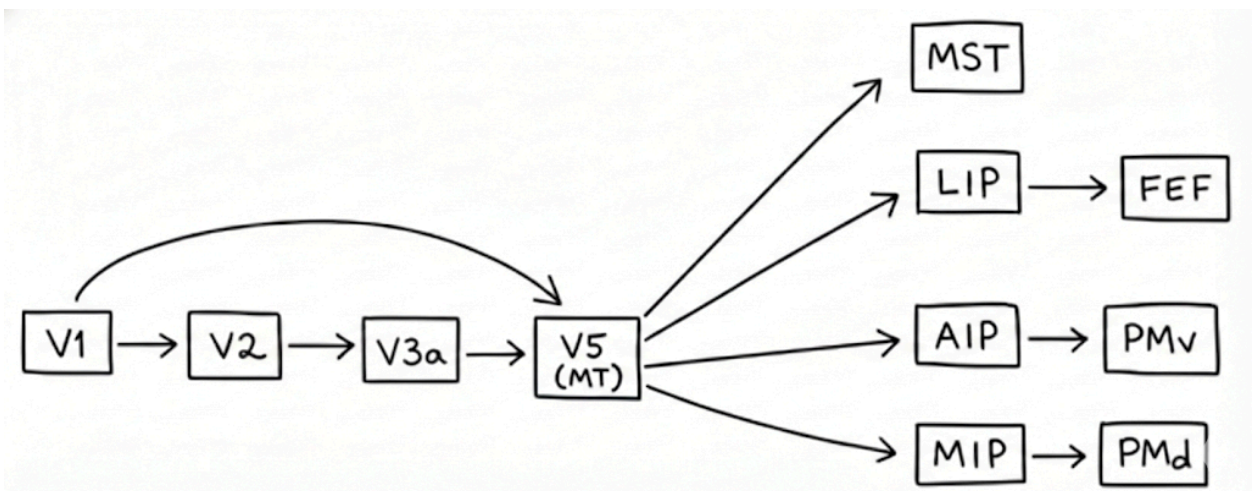
2. Vision

- **From eye to cortex.** Light is transduced by photoreceptors in the retina into neural signals. These are relayed to the thalamus before reaching the cortex. (Auditory signals follow a parallel route from the cochlea.)
- **Thalamus.** The central relay station for sensory input. For vision, the relevant subregion is the lateral geniculate nucleus (LGN).
 - **Lateral geniculate nucleus (LGN):** a six-layered structure receiving input from retinal cells via the optic nerve. Preserves retinotopic organization and projects to V1. Receives extensive feedback from the cortex.
- **Division of visual input.** The optic nerves from the two eyes converge at the optic chiasm, an X-shaped crossing point, and inputs are divided up. Two retinal images (A and B) are divided in Left/Right fields; L/R fields from two eyes are combined into R(A)/R(B) and L(A)/L(B), and each is processed by the opposing hemisphere of the cortex.
- **Visual cortex.** A large family of cortical areas devoted to vision, primarily in the occipital lobe but extending into the temporal and parietal lobes.
- **Functional specialization.** This is the idea that specific localized areas in the brain take on specific tasks. The rise of functional specialization as a framework for understanding the brain was one of the great discoveries of 20th-century neuroscience.
- **Primary and secondary visual cortex.** Most visual signals pass through these two key areas:

- **V1 (primary visual cortex, striate cortex):** first cortical area to receive input from the LGN. Edge orientation, spatial frequency, color, binocular disparity, direction of motion. Precise retinotopic map.
- **V2:** surrounds V1. Contour integration, figure-ground segregation, illusory contours. Retinotopic.
- **Ventral stream:** “vision for description”. A pathway running from the occipital lobe ventrally (downward) into the temporal lobe, object- and category-oriented outputs



- **Regions:**
 - **V1 + V2**
 - **V4:** color perception and intermediate form processing (curvature, figure-ground segregation, contour integration, texture).
 - **IT (inferotemporal cortex):** end-stage of the ventral stream. High-level object recognition, face perception, visual categorization. Contains the fusiform face area (FFA) and parahippocampal place area (PPA).
- **Upper-visual-field bias:** ventral areas tend to preferentially represent the upper visual field. Consider the kinds of perceptual tasks involved in the upper field.
- **Dorsal stream:** “vision for action”. A pathway running from the occipital lobe dorsally (upward) into the parietal lobe, with action-oriented outputs.



- **Regions and sequences:**
 - **V1 → V2**
 - **V3a:** dynamic form—shapes defined by motion.
 - **V5 (MT):** visual motion: speed and direction. Central to the dorsal stream.

- **MST**: optic flow and personal space.
 - **LIP** (lateral intraparietal area) → **FEF** (frontal eye field): Planning (LIP) and execution (FEF) of eye movements.
 - **AIP** (anterior intraparietal area) → **PMv** (ventral premotor cortex). Visual processing of object shape for grasping → planning and execution of grasping.
 - **MIP** (medial intraparietal area) → **PMd** (dorsal premotor cortex). Visual encoding of reach targets → planning and execution of reaching.p
- **Lower-visual-field bias**: dorsal areas preferentially represent the lower visual field. Consider the role of hands in action, and the importance of perceptually monitoring our hands.
- **Feed-forward vs. feedback connections**. Visual processing is often described as feed-forward: $V1 \rightarrow V2 \rightarrow V4 \rightarrow IT$. But there are roughly 5–10x as many feedback connections as feedforward. These are thought to be involved in attention, prediction, and contextual modulation– but the real explanation remains unknown.

3. Maps in V1

- **V1 as a site of multiple maps**. V1 contains several overlapping maps, each encoding a different visual property:
 - **Retinotopic map**: spatial map of the visual field; neighboring neurons respond to neighboring locations.
 - **Orientation map**: a map of edge orientations. Neurons tuned to specific orientations (vertical, horizontal, 45°, etc.), arranged systematically across the cortical surface.
 - **Ocular dominance columns**: alternating bands preferentially responding to left or right eye. Roughly striped pattern across the surface.
 - **Color blobs**: clusters of neurons sensitive to color, interspersed among orientation-selective regions.
- **Orientation maps in detail**.
 - **Hypercolumns**: an idealized unit of cortical organization containing a full set of orientation-selective neurons for one small visual-field region, and a color blob; a complete local analysis of a small patch.
 - **Pinwheel organization**: within each hypercolumn, orientation preferences rotate smoothly around a central singularity point.
- **Cortical layers**. V1 has six principal layers (numbered 1–6, surface inward):
 - **Layer 1**: outer layer; few cell bodies; mostly wiring.
 - **Layer 2/3**: complex computations; lateral connections; main output to higher cortical areas.

- **Layer 4** (especially 4C): main input from the LGN; simple computations, local comparisons; main output to 2/3.
 - 4C α receives magnocellular input (motion, coarse form); 4C β receives parvocellular input (color, fine detail).
- **Layer 5**: projects to subcortical structures.
- **Layer 6**: feedback to the LGN.
- (For our purposes, **layer 4C** (input processing) and **layers 2/3** (output processing) are most important. Information arrives from the LGN at 4C, is transformed, then passed to 2/3 for transmission to the next cortical area.)
- **Hierarchy of cell types:**
 - **Simple cells**: respond to oriented edges at a specific position in the receptive field. Predominantly layer 4C. First extraction of orientation information.
 - **Complex cells**: respond to oriented edges regardless of exact position—orientation-selective but position-invariant. Layers 2/3.
 - **Hypercomplex (end-stopped) cells**: respond to edges of a specific length; response decreases if the stimulus extends beyond. Detect corners, endpoints, curvature. Layers 2/3.

4. Retinotopy

- **Receptive field.** A neuron's receptive field is the region of the visual field in which stimulation produces a response in a given neuron.
- **Retinotopy.** A cortical area is retinotopically organized if there is a systematic mapping from positions in the visual field to positions on the cortical surface, such that nearby neurons in the cortex have nearby receptive fields in visual space.
- **The cortical image.** The V1 retinotopic map represents the contralateral half of the visual field. The image itself is continuous but distorted, magnifying around the center of the visual field.
- **Aside: why "retinotopy" is a misnomer.** What is mapped is not the retina but the visual field. The term is inherited from the retinal origin of the mapping, but the cortical map does not duplicate retinal structure. Ocular dominance columns show that left-eye and right-eye inputs are interleaved—the map is of a unified visual-field representation from both eyes.
- **Reading retinotopic imaging.** In fMRI retinotopic mapping, the visual field is described using two coordinates:

- **Polar angle:** angular position around fixation (upper, lower, left, right). Mapped with a rotating wedge stimulus. Produces a polar-angle gradient across the cortical surface.
- **Eccentricity:** distance from fixation. Mapped with an expanding/contracting ring. Produces an eccentricity gradient.
- Together, these gradients specify a complete visual-field map.
- Reversals in the polar-angle gradient identify boundaries between adjacent areas (V1/V2, V2/V3, etc.).
- **Cortical magnification.** The foveal region is represented by much more cortex than the periphery. The magnification factor (mm of cortex per degree of visual angle) is highest at the fovea and decreases with eccentricity. Reflects the greater density of photoreceptors and ganglion cells at the fovea.
- **Retinotopy across visual areas.** Retinotopic maps extend well beyond V1: V2, V3, V3A, V4, and into higher areas of both the ventral stream (V8, VO) and dorsal stream (V3A, V5/MT, V6).
- **Retinotopic feature hierarchy.** Two systematic changes across the visual hierarchy.
 - Receptive field size increases: V1 neurons respond to tiny patches, IT neurons to most of the visual field.
 - Feature complexity increases: V1 encodes oriented edges, IT encodes objects and categories.
- **Retinotopy and orientation maps.** In V1, the retinotopic map and the orientation map are overlaid on the same surface. Since both are 2D maps, fitting them together appropriately creates a theoretical and practical challenge.
- **Is retinotopy just another map?** Neuroscientists tend to talk about retinotopy as just one more map in V1, alongside orientation and ocular dominance. But it has a distinguished status, since it provides the spatial scaffold within which all other maps are organized. Every other map in V1 is laid out in retinotopic coordinates.