The visual system: from the retina to early visual areas

Whilst we heavily rely on our vision to interact with our environment and perform everyday life actions, most of the time we do not realise how complex the visual machinery might be. What underlies this ability that most species have to visually perceive the world? How does a nervous system, the brain in our case, manage to make sense of the light information that comes and hits the retina?

These questions are far from being new as already Plato and Galen had their own views on the matter. From the extramission theory, once claiming that the eye emits light to encompass objects, to the intromission theory introduced during the Islamic Golden Age by Ibn al-Haytham (Alhazen) and Ibn Sina (Avicenna) that was finally stating that the eye is using the light to provide visual perception, it was only during the early 17th century with Kepler's work that we approached the idea of a camera obscura, with an image being projected on the retina.

The metaphor of the camera works well to grasp the anatomy of the mammal eye and explain the role of the different elements that compose it.

As illustrated on Figure 1, the light –in the form of an electromagnetic wave – first goes through the cornea, a fixed transparent membrane in charge of about 70% of the light refraction and that covers the iris and the pupil. The muscular action of the iris will allow more or less light to enter the eye by constricting (miosis) or dilating the pupil (mydriasis), a phenomenon also known as the pupillary light reflex. The second step is the aqueous humour, a watery fluid that provides nutrients to the cornea.

The light will then go through the lens, a biconvex structure composed of different layers and that further helps to refract the light by accommodating under the action of ciliary muscles, doing the same work as the focus of a camera. Ciliary muscles will contract for a short distance, thus bending and thickening the lens, giving it a strong refraction power, and they will relax for a far distance, then stretching the lens. Finally, the luminous information will cross the vitreous humour, a sort of jelly that gives the eye its round shape before reaching the retina and the cells that it is made of.

Located in the back of the eye, the retina is in charge of transforming the light information into a signal that will be interpreted by the brain, that is an electric signal. Among the different cell layers retina is made of (see Figure 2), the photoreceptor layer represents the initial step of signal conversion. Photoreceptors are divided into two categories: rods and cones.

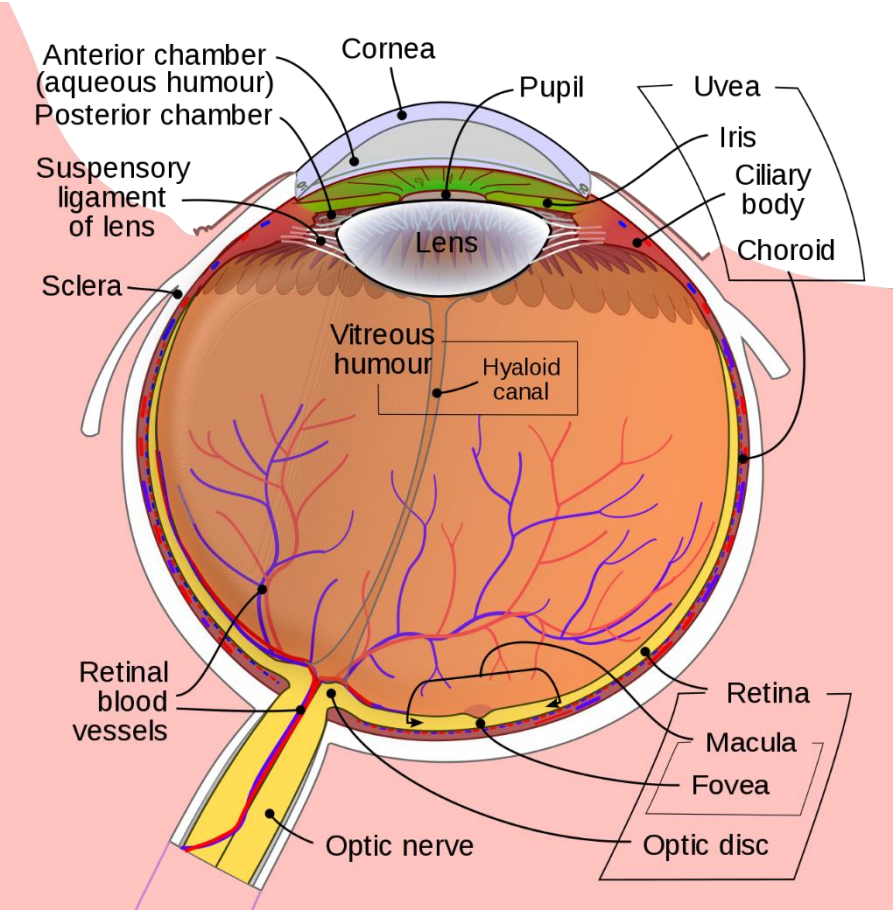

Figure 1: Anatomy of the eye.

The mammal eye is made of different elements that help refract the light to be focused on the retina. The light, in the form of an electromagnetic wave, first goes through the cornea, in charge of about 70% of refraction, crosses the aqueous humour, a watery liquid that provides nutrients to the cornea, then goes through the lens, a biconvex structure that further refracts the light by accommodating, and finally crosses the vitreous humour, a sort of jelly matter that gives its round shape to the eye, before hitting the retina and the different cells that compose it. The most detailed information is projected onto one specific part of the retina: the fovea, where signal processing is finer, due to the asymmetrical retina cell distribution (detailed further in the text).

Rods are mostly responsible for dim light vision and represent the majority of photoreceptors (95% of them, that is about 120 millions), whilst cones are more sensitive to bright and coloured light, being themselves divided into three different types: short wave-length (blue colour), medium wave-length (green colour), and long wave-length (red colour) sensitive cones. The distribution of rods and cones varies across the retina, with most cones being in the centre of

the retina, at the fovea level, and rods being more highly dense in the periphery surrounding the fovea. A chemical cascade reaction, known as photo transduction (see Figure 3 for more details), is the result of photon detection within the outer part of the photoreceptor cells that contain photoreceptor pigments (rhodopsin in rods and photopsin in cones), leading to an hyperpolarisation of photoreceptor cells that further conveys the now-electric message, in the form of a membrane potential, to the next layer made of bipolar and horizontal cells.

From photoreceptors to bipolar cells, the information is compressed due to a lesser number of bipolar cells than of photoreceptor cells and the resolution varies depending on the type of photoreceptors. High numbers of rods in the periphery of the retina converge onto single bipolar cells, whereas cone information from the retina is less compressed, thus giving rise to a high-resolution vision at the fovea level. This difference will be preserved at the brain level, since proportionally more optic nerve fibres, made of the axons of ganglion cells, will conduct information from the cones, giving a primary importance to the information projected on the fovea.

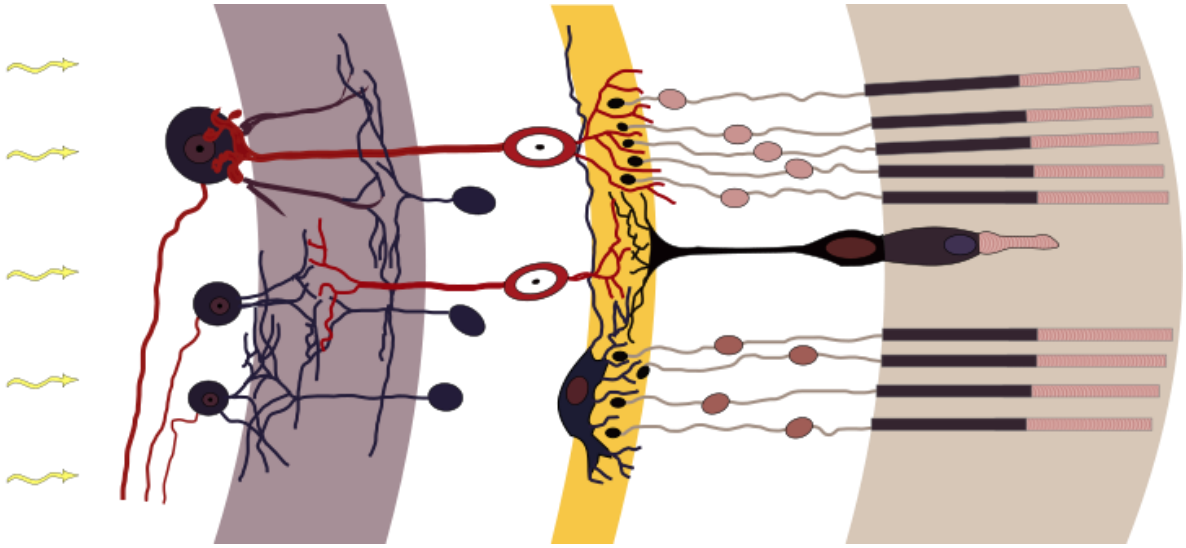

Figure 2: Retina cell layers.

Light (yellow arrows on the left) goes through the different layers in the retina before reaching the photoreceptor layer (beige layer, on the very right). The information encoded by photoreceptors (cones in the fovea and rods in the periphery) is then back propagated to the bipolar and horizontal cells (the outer plexiform layer, in yellow) and further sent to the ganglion cells (the inner plexiform layer, in purple) before leaving the retina through optic nerve fibres made of the axons of ganglion cells.

Each retina cell encodes a spatial localisation of the visual space, that is one cell's baseline state will be modified in response to the presence of light in one part of the visual field only, leading to a modification of the cell's membrane potential or a generation of action potentials. This cell sensitivity area is its receptive field. The size of those receptive fields varies accordingly to the visual cell hierarchy, becoming bigger and bigger as one goes up the layers of the visual system. Photoreceptors are their own receptive field, as they will be triggered by luminous information received in their outer segments localised in one physical point of the retina on which visual space is projected. Photoreceptors are connected to bipolar cells and they will then represent the receptive fields of those bipolar cells. Several bipolar cells are also connected to a ganglion cells and they will again compose the receptive field of this ganglion cell. The receptive field of the ganglion cell is thus a collection of the sensory inputs that are received by all the photoreceptors that are synapsing with the bipolar cells that are connected to the ganglion cell. This convergence process will continue up to brain neuron cells, leading to bigger and bigger receptive fields.

Receptive fields are not simply defined as a region getting excited by light. From bipolar cells onwards they also have an ON-OFF organisation, having one or several excitatory parts and one or several inhibitory parts. Their shape varies from being circular at the retina level to being more elongated once at the cortex level, becoming more sensitive to the light orientation.

Bipolar cells for instance have an antagonist centre-surround organisation, with two possible configurations: an ON-centre associated with an OFF-surround or an OFF-centre coupled with an ON-surround. Located between photoreceptors and bipolar cells, horizontal cells will selectively inhibit the information of some photoreceptors, only allowing strongly emitting photoreceptive cells (i.e. photoreceptors receiving the highest amount of light) to transmit their signal to the bipolar cell they are connected to, thus increasing the signal-to-noise ratio. They are directly involved in the centre-surround organisation of the bipolar cells as they mediate the surround activity of the bipolar cells. The ON-OFF configuration of bipolar cells and the lateral inhibition property of horizontal cells represent the first step in the detection of edges and contrasts in the visual information received at the level of the retina.

Ganglion and amacrine cells compose the last step before the information leaves the retina through the optic nerve fibres made of the axons of ganglion cells.

Part of the inner plexiform layer like ganglion cells, amacrine cells are interneurons that are involved in integrating and modulating temporal information to transmit it to the ganglion cells.

They might also play a similar role as of the horizontal cells in varying the signal from adjacent ganglion cells to enhance signal-to-noise ratio.

Ganglion cells are subdivided into three main categories: magnocellular (M-type), parvocellular (P-type), and koniocellular (K-type) ganglion cells. They all have distinct properties and will follow different pathways. This segregation will remain until the very end of signal integration and processing.

Magno-type and parvo-type cells share complementary properties and are usually taught to be part of the "where" pathway with a high temporal resolution and the "what" pathway with a high spatial resolution, respectively.

Parvocellular ganglion cells represent the vast majority of ganglion cells (about 80%). Of small size in term of dendritic tree size, they are also known as midget cells. Mostly connected to cones, they receive visual information in a one-to-one fashion within the fovea and the parafoveal area, that is, one ganglion cell is receiving information from one bipolar cell, which also receives information from a very low number of photoreceptors. Due to this specific configuration, the parvocellular pathway conveys very precise visual information, leading to a great detection of edges and thus, to the later integration of shapes. Their centre-surround organisation also supports the discrimination of antagonist green-red colours.

Magnocellular ganglion cells integrate an achromatic visual signal sent by bipolar cells and modulated by amacrine cells faster than parvocellular cells. They are also called parasol cells due to the vast size of their dendritic tree and of their receptive fields, making them great motion detectors. They represent about 10% of the ganglion cells.

Koniocellular ganglion cells are the 10% remaining ganglion cells and represent 8-10% of the cone cell population. S-cone cells are physiologically and anatomically very different from L- and M-cones cells found in the parvocellular pathway, from the outer plexiform layer onwards (bipolar, horizontal, and ganglion cells). Often presented as having heterogeneous properties, koniocellular ganglion cells are the less studied and are believed to be an archaic form of the more recently evolved magno- and parvocellular ganglion cells. They underlie yellow-blue colour discrimination via their antagonist centre-surround organisation.

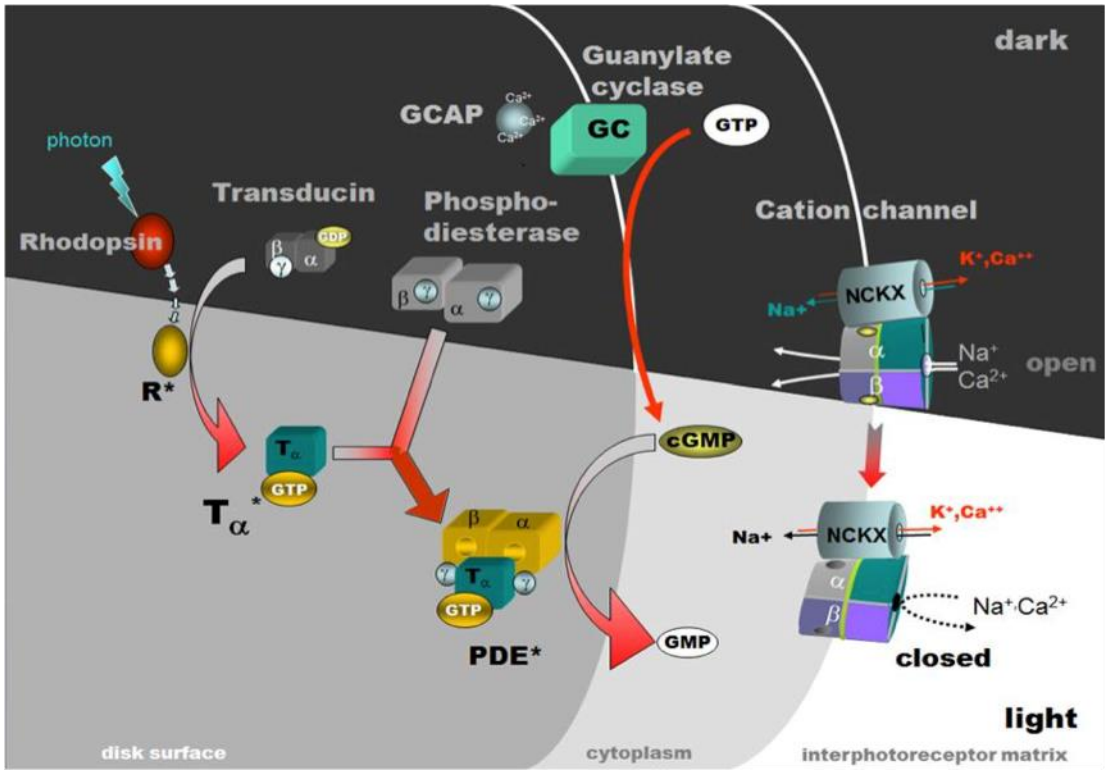

Figure 3: Phototransduction.

Photoreceptors baseline state is within dark conditions, photoreceptors are then depolarised due to high level of cGMP keeping sodium gates open. This allows potassium ions to get out of the cell and sodium to get in, creating what is called a dark current. A neurotransmitter, glutamate, is then released by the photoreceptor. The action of glutamate is to hyperpolarise ON-centre bipolar cells and to depolarise OFF-centre bipolar cells (for sake of simplicity, we will not mention the horizontal cell pathway). Once a photon is detected by a photopigment present in the disks of the outer segment of a photoreceptor (here, the rhodopsin), it triggers a whole chemical cascade as illustrated on the figure. Briefly, the retinal component (a vitamin A derivative) of the rhodopsin molecule becomes activated (R*), changing configuration from 11-cis to all-trans. To balance this change, opsin, the other component of rhodopsin, also undergoes a configuration change becoming metarhodopsin II. Metarhodopsin II then activates the transducing protein, causing its dissociation from GDP and its binding to GTP. The alpha subunit of transducing Tα* dissociates from the other subunits but remains attached to the binding GTP. This complex will then activate the cGMP-hydrolysing phosophodiesterase (PDE*) responsible for the degradation of cGMP in GMP. As a consequence, cGMP concentration within the cell decreases, leading to the closing of cGMP-dependent sodium gates, thus stopping the dark current and causing the hyperpolarisation of the photoreceptor cell. Glutamate is no longer released in big quantities and ON-centre bipolar cells depolarise whilst OFF-centre bipolar cells hyperpolarise.

The axons of the different types of ganglion cells form the optic nerve fibres. Leaving the retina at the level of the optic disc, they mostly carry visual information to the lateral geniculate nuclei (LGN), a 6-layer structure located in the thalamus (see Figure 4). Before reaching the LGN, about 60% of the optic nerve fibres decussate at the level of the optic chiasma. This will have consequences for the processing of the different parts of the visual field. As illustrated on Figure 5, the information received by the nasal retinae will be processed by the contralateral LGN and visual cortex, whereas the ipsilateral visual cortex will process the information received by the temporal retinae. This implies that one visual hemifield is seen by both eyes and will be processed by the contralateral LGN and the contralateral visual cortex. It is also worth noting that the temporal retinae receive information from the central visual field where information seen by both eyes overlaps, thus supporting binocular vision.

Information processed at the level of the LGN is segregated, based on the type of cells conveying it. Parvocellular ganglion cells will project in the dorsal layers of the LGN (layers 3 to 6), magnocellular ganglion cells project in the ventral layers of the LGN (layers 1 and 2), and koniocellular ganglion cells project between layers. Moreover, layers 2, 3, and 5 will process ipsilateral information, whereas layers 1, 4, and 6 will process contralateral information, thus keeping the information received in each visual hemifield separated.

Axons of LGN relay neurons that transmit retinal information to the primary visual cortex compose part of the optic radiations, forming the link between the retinogeniculate and the geniculocortical pathways. LGN output to the primary visual cortex is quite similar to its retinal input, although precise convergence and divergence of the information still remains unclear. Feedback connections from the primary visual cortex to the LGN form another major portion of optic radiations and most of the input of the LGN and are possibly involved in information filtering.

The primary visual cortex or V1 is the first cortical structure involved in visual processing. Located in the occipital lobe at the back of the primate brain, it is made of 6 different layers that will be the target of LGN inputs in a differentiate manner: Magnocellular cells first project onto the 4Cα layer of V1 and then onto the 4B layer where direct connections to area MT (medial temporal area, known for processing motion, see e.g. Newsome and Pare, 1988) exist; parvocellular cells project onto the 4Cß layer of V1 and further on the 2nd and 3rd layers within the blobs and in between blobs; koniocellular cells directly projects into the blobs of the 2nd and 3rd layers. The 6 different layers of V1 are further subdivided in columns. Ipsilateral and

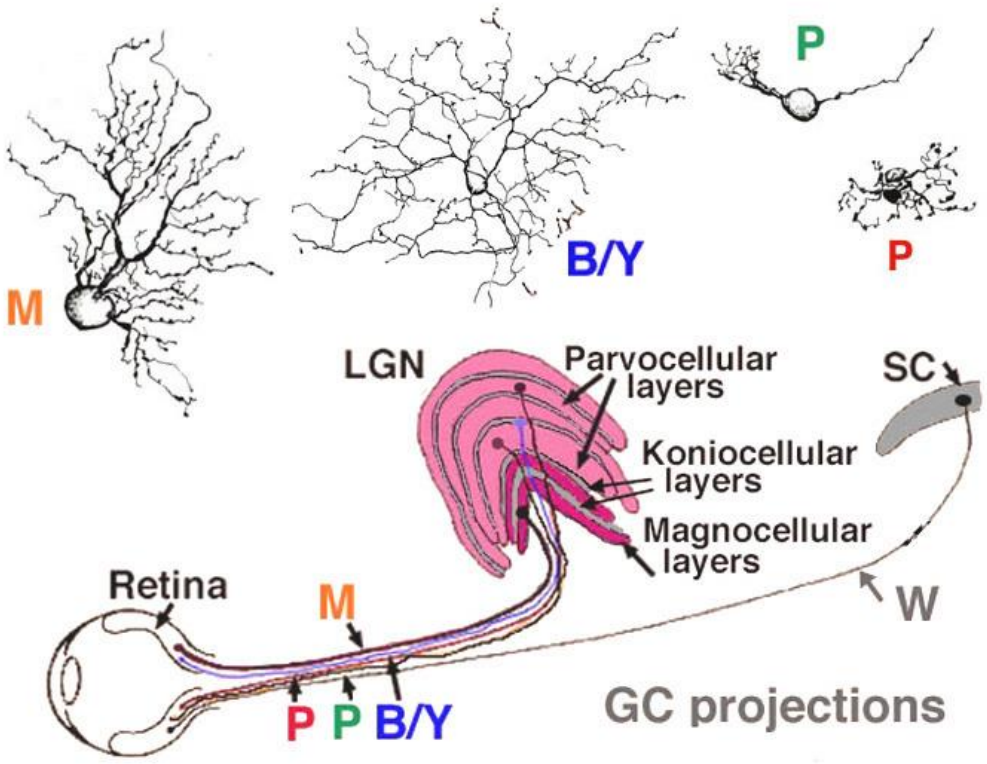

Figure 4. Projections of ganglion cells to the lateral geniculate nucleus (LGN).

Top half: representation of the different types of ganglion cells found in the retina: M-type (magnocellular pathway), P-type (parvocellular pathway), and B/Y or K-type (koniocellular pathway) cells. Dendritic tree differences appear clearly. Bottom half: M-type, P-type, and K-type (B/Y on the figure) ganglion cells project onto different layers in the LGN, keeping the information they convey segregated. Adapted from Dacey and Peterson (1992) & Shapley and Perry (1986). Retrieved from Webvision (Helga Kolb).

contralateral projections from the LGN will be kept segregated within adjacent columns of layer 4C. Those columns have been called ocular dominance columns (LeVay, Hubel, & Wiesel, 1975).

Contrary to the retinal cells, V1 cells receptive fields are more elongated. Their size and properties vary depending on the complexity of the cell and on the layer where the cell is located. Hubel and Wiesel (1968) distinguished two kinds of cells: simple cells and complex cells. Simple cells are mostly located in layer 4 and have small receptive fields with a monocular input. They have a clear ON-OFF organisation, which can follow a centre-surround organisation or being more lateralised with a spatial offset. Those neurons are selective for a

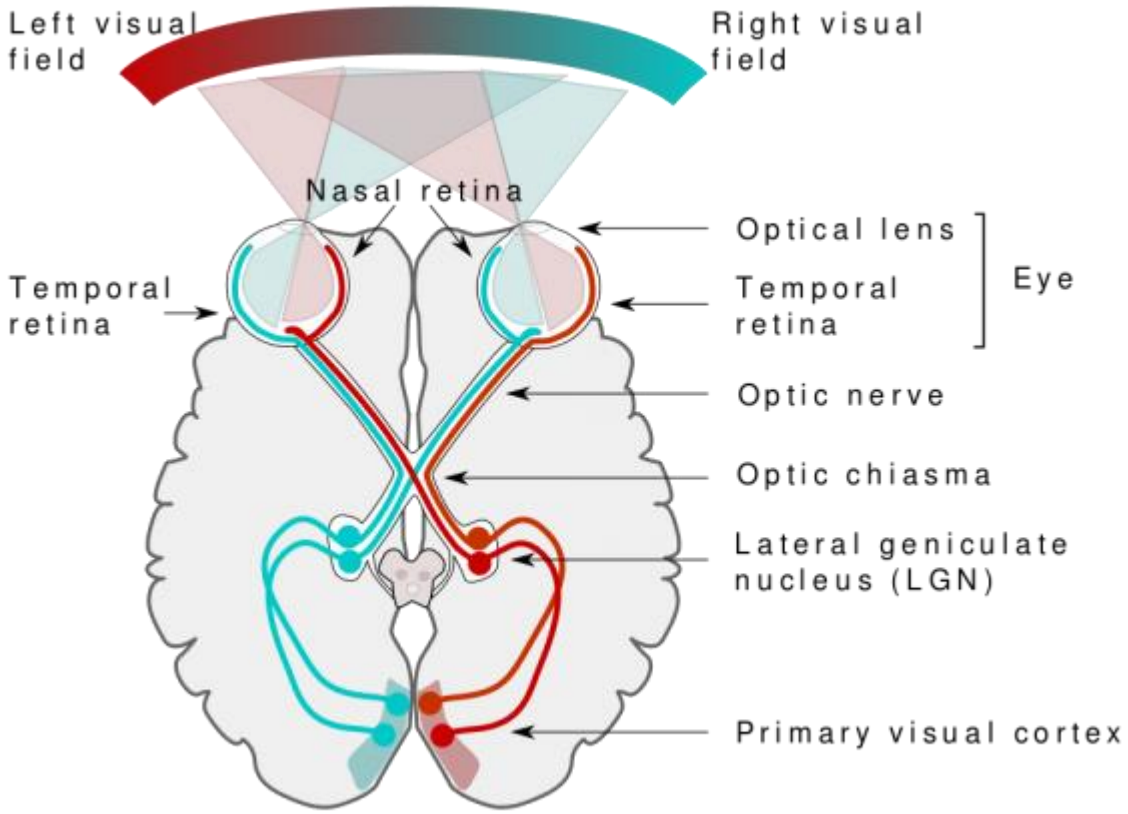

Figure 5: Visual pathway, from the retina to the primary visual cortex.

Hemifields and how the information is conveyed to the primary visual cortex.

spatial orientation perfectly aligned with their receptive fields. In layers 2, 3, 5, and 6, cells become more complex: their medium sized receptive fields do not have any clear ON-OFF organisation anymore and they display binocular responses, leading the path to binocular visual integration (Cumming and Parker, 2000). Those complex cells are selective for spatial orientation with less constrain than the simple cells: Stimulation can occur whenever in the receptive field; the cell will fire as long as the stimulation remains aligned with its receptive field orientation. Cells selective to a same orientation will be gathered in a single orientation column.

Besides this columnar organisation, the primary visual cortex also has a retinotopic organisation. Each point of the visual field that is projected on the retina has its corresponding processing surface in V1. The ipsilateral hemifield projects on the contralateral primary visual cortex and the superior hemifield on the inferior part of V1. The foveal region that projects on the posterior part of V1 is overrepresented, due to cortical magnification: the cortical

representation of the fovea in V1 projects onto a much larger region than the actual size it occupies in the retinal space. As a direct consequence of this cortical magnification, the more peripheral areas are represented on a smaller cortical surface than the surface they actually occupy in the retinal space. This correspondence between the retina and the primary visual cortex is repeated in each of V1 hypercolumns, which correspond to all the different orientation columns (i.e. a complete 180° sequence) or to each complementary duo of ocular dominance columns (i.e. representing both left and right eyes) (Hubel & Wiesel, 1977). This retinotopic organisation will be also present in extrastriate visual areas (i.e., areas belong the primary visual cortex, also called the striate visual cortex), with a notable difference in the size of receptive fields: the higher in the visual hierarchy, the bigger the size of neuron receptive fields, and the more coarse-grained the retinotopic mapping. This has as a direct consequence a complexification of the visual features being extracted.

As a matter of fact, the information collected at the retina level is not only involved in visual perception per se but is also used for three different functions: the pupillary reflex, with information converging into the pretectum; the circadian rhythm with the suprachiasmatic nucleus as the relay centre; the coordination of head and eyes movements and saccade planning, with the remaining optic nerve projections reaching the superior colliculi before being further processed by cortical structures.

From early visual areas to higher visual areas: two pathways

Visual information entering but also leaving the primary visual cortex is segregated into two parallel pathways[1]: the magnocellular (dorsal) and the parvocellular (ventral) pathways. Neuropsychology and brain lesion studies have helped a lot in the understanding of how those different pathways might complement each other and in shedding light on the specialisation of some brain areas. For instance, cortical lesions in areas on the dorsal stream were associated with various visuo-motoric or visuo-spatial disorders whereas lesions on the ventral pathway led to object recognition deficits or to acquired achromatopsia.

The magnocellular pathway is more generally involved in processing spatial information of visual objects: their movements, the distance they are located at, or their distance relationship; in order to enable interactions with those objects. Also called the “where” pathway, it

[1] The koniocellular pathway will not be further detailed, due to a limited knowledge about this pathway.

comprises a network of areas located on the occipito-parietal (dorsal areas) side of the brain. The medial temporal area (MT) and then the medial superior temporal area (MST) are the first cortical areas to receive inputs from V1. Part of the MT complex (the MT cluster in macaques, and the hMT+ cluster in humans[2]) that also includes the fundus superior temporal area (FST) and V4t, those areas are mainly involved in processing motion information. Higher visual areas of the dorsal pathway, located in the infero-parietal cortex (Shikata et al., 2007), will be involved in visually guided movements, such as reaching and grasping objects (e.g., the anterior infero-parietal area, AIP; Taira et al., 1990; Sakata et al., 1995), or in eye movement planning (e.g., the lateral infero-parietal area, LIP; Andersen et al., 1990).

The parvocellular pathway, or the "what" pathway, involves areas located more ventrally, in the occipito-temporal part of the brain. Those areas, such as V4 (Zeki, 1974) or the infero-temporal area (Conway et al., 2007; Bartels and Zeki, 2000), are involved in the processing of form, shape, and colour perception and, to a further extent, objects identification or recognition. As an example of the specialisation of the occipito-temporal and infero-temporal cortices, some areas showing strong responses to objects (e.g. the lateral occipital complex, LOC), scenes (e.g. the occipital place area, OPA), or faces (e.g. the face fusiform area, FFA) have been extensively studied, establishing a robust selectivity for those objects (Kanwisher, McDermott, and Chun, 1997; Grill-Spector, Kourtzi, and Kanwisher, 2001; Park and Chun, 2009; Dilks, Julian, Paunov, and Kanwisher, 2013).

Not only those two pathways differ in the kind of information they process (Livingstone & Hubel, 1987), they also have different processing speed, with the magnocellular pathway being faster (high conduction velocity and transient responses) than the parvocellular pathway (low conduction velocity and sustained responses). This distinction along with a parallel processing of information underlies a coarse-to-fine processing of the visual information where low spatial frequencies carried by the magnocellular pathway are processed first by the visual system and will then serve as a feedback for the integration of higher spatial frequencies, brought by the parvocellular pathway, resulting in a finer processing of visual information (Marr, 1982; Schyns and Oliva, 1994; Bullier, 2001; Bar, 2004). Now supported by empirical evidence (see e.g., Lu et al., 2018; Petras et al., 2019), this integration theory of the visual signal challenges the traditional views of a purely feedforward signal and sheds light on the dynamics of the visual system and the importance of feedback connexions.

[2] Nomenclature conventions: h = homologous area, p = putative (homologous) area.

In a nutshell, although some brain areas are very specialised and necessary for the processing of some specific types of information, as for the MT area and its primordial role in motion processing, the brain is generally organised as a hierarchical network with numerous feedforward but also feedback connexions (**Error! Reference source not found.**; Van Essen & DeYoe, 1995).

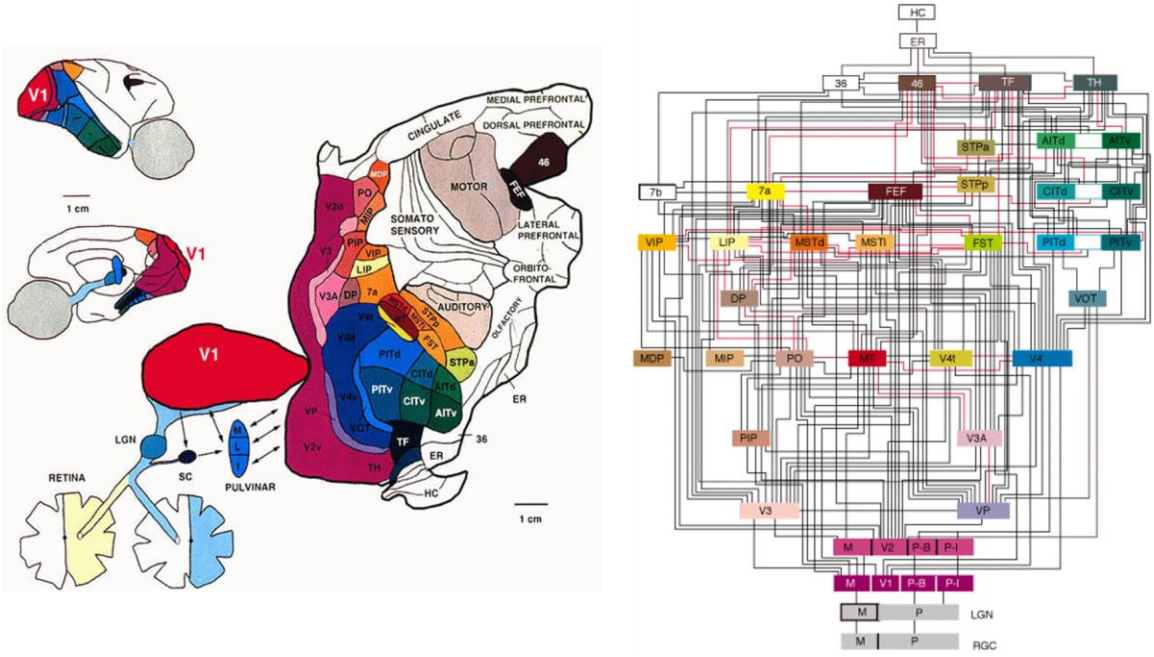

Figure 6. Hierarchical organisation of the visual system, based on Felleman and Van Essen 1991.

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