Visual processing

Brian A. Wandell[a] **and Jonathan Winawer**[b], [a] Stanford University, Stanford, CA, United States; and [b] New York University, New York, NY, United States

Key points

- Light encoded by the retinal photoreceptors is processed by multiple circuits, each serving a specific purpose.
- These circuits transmit information to different brain regions and handle distinct functions including eye movements, pupil response, circadian rhythms, and scene interpretation.
- The most prominent pathways, responsible for visual processing, project via the thalamus to the posterior visual cortex. Multiple maps and areas in the posterior cortex interpret the scene.
- Visual processing principles appear to reduce redundancy, using sparse and asynchronous signals that compare features in many different areas, later integrated into a cohesive whole.

Abstract

The human visual system is a network of neural components that combine to create our perception of the world and guide our behavior. Deciphering the computational principles of this system is an important scientific challenge. We review measurements of these components, from the retinal encoding to cortical circuitry, and from molecules to circuits, focusing on measurements that are relevant to visual processing. We then delve into principles proposed to explain how this diverse collection of visual components enables us to interpret our surroundings.

Introduction

How the brain encodes and interprets the visual scene, enabling us to navigate, recognize people and objects, read, and enjoy a beautiful environment, is a grand challenge of vision science. Helmholtz famously noted that visual processing of the encoded signal is an "unconscious inference"[1] (von Helmholtz, 1925). Perhaps he opened his Handbook with this thought because at that time it was widely believed that we see what is there. In contrast, he recognized that our visual experience is an interpretation created by the brain.

In explaining unconscious inference, Helmholtz brought the concepts of the physical and perceptual world together: perceptions are inferences that are consistent with the properties of the physical world.

> The general rule determining the ideas of vision that are formed whenever an impression is made on the eye, is that such objects are always imagined as being present in the field of vision as would have to be there in order to produce the same impression on the nervous mechanism
> (Italics in the original; Southall, Physiological Optics, Vol. III, p. 2, 1865).

The word unconscious acknowledges that the neural processing that interprets the scene can not be revealed by introspection. The tools of neuroscience—including anatomy, functional MRI, electrophysiology, and psychophysics—are our only hope for measuring the neural processing principles that produce our visual experience.

At the time Helmholtz wrote, neuroscience measurements were primitive. Detailed analysis of how central neural mechanisms influence perception had to wait for advances in neuroscience instrumentation. Modern instrumentation has reached an extraordinary level, and visual neuroscience is now rich with data beyond what Helmholtz might have imagined. The challenge modern vision scientists have is how to make sense of the data in terms of visual processing principles.

To do this, David Marr famously advised that we separate the analysis of visual processing into several levels (Marr, 2010). One part identifies the visual system goals, a second expresses the algorithms used to achieve those goals, and the third describes the neural implementations of the algorithms. In this chapter, we work our way up through these levels. The first section (Anatomy and Signals) reviews key visual anatomical and functional signals that implement the unconscious inferences. The second section (Processing Principles) describes visual processing algorithms that may be implemented by these neural systems. The third level, computational goals, are discussed as we describe each of the systems.

The neural structures and signals we present suggest principles the brain may use for visual processing. Similarly, the principles we present suggest neural implementations. Finally, we are well aware that our field is missing some basic principles; hence, a further goal of this contribution—really the main goal—is to spur thinking about new principles and neural substrates that remain to be discovered.

Anatomy and signals

To understand the principles implemented by a visual system component, we must know its place within the overall system. What are its inputs? Where does it send its outputs? For example, we could not understand the retina without understanding optics and light; to understand the primary visual cortex we must know where it sends its output axons. For this reason, we begin with a description of the system architecture of the human visual system. We then describe the major components in more detail.

System overview

The physiological optics and the two retinae measure an image of the electromagnetic radiation in the scene (**Fig. 1**). Radiation at wavelengths shorter than 380 nm do not reach the retina because they are absorbed by the lens. Beyond 780 nm, the photoreceptor photopigments have very little sensitivity. Hence, the electromagnetic radiation encoded by the eye (light)[2] is mainly in the wavelength range from 380 nm to 780 nm.

The physiological optics include the cornea and lens. The cornea has a fixed optical power (40 diopters), comprising about 2/3 of the total optical power in the eye; the lens accounts for the other third (20 diopters). In most young people the lens shape accommodates to bring objects at a specific distance into focus at the level of the inner segments of the retinal photoreceptors. The ability to accommodate declines as people age (presbyopia). The photoreceptor inner segments guide the light towards the photoreceptor outer segments, which contain photopigments that absorb the light. The absorption initiates a cascade of chemical events including a membrane photocurrent and neurotransmitter release at the synapse (Lamb and Pugh, 2006).

[1] Also translated as an unconscious conclusion in the OSA version.
[2] "Light" is the electromagnetic radiation encoded by the eye.

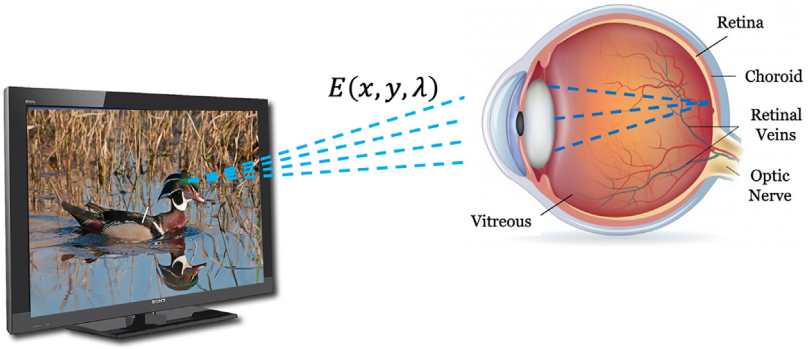

Fig. 1 The spectral radiance from each image point, E(x,y,λ), sends a bundle of rays to the pupil of the eye. The cornea and lens bend the rays and form a retinal image (retinal spectral irradiance). The lens accommodates (changes its shape) to bring points at different distances into focus. The eye focuses light in the wavelength range 500–600 nm. Other wavelengths, particularly around 400–450 nm are not well focused (chromatic aberration). Modified from Wandell et al. (2022).

The retina is roughly a 3.6 cm diameter disk (~1100 mm^2) that lines the back of the eye. It contains five major neuronal cell types: receptor, bipolar, ganglion, horizontal, and amacrine (**Fig. 2**B and C). Over most of its extent, these cells are organized into three primary layers (Rodieck, 1998). The photoreceptors play a special role because their inputs are light and their outputs are chemical (neurotransmitter release, **Fig. 2**A). The photoreceptor outputs are processed by multiple circuits, formed by combinations of the 4 other retinal cell types.

The retina, unlike other sense organs such as the cochlea and skin, receives no inputs from the brain. The feedback from the brain to the eye is in the form of motor signals that control head-eye position, pupil size, and lens accommodation.

The retinal ganglion cells (RGCs) are the output neurons of the retina. The RGC axons exiting the left and right retinae form the two optic nerves (**Figs. 3 and 4**). These nerves converge (but do not communicate) at a midline location between the two hemispheres—the optic chiasm—where they are sorted into two groups. The axons from the nasal side of each retina cross to the opposite hemisphere, joining with axons from the temporal side of the contralateral retina. The sorted axons after the chiasm form the two optic tracts. A consequence of this sorting is that the left and right hemispheres receive signals from both eyes, and the signals in each hemisphere are initiated by light from the contralateral visual field.

The optic tract includes axons that terminate in multiple regions (**Fig. 3**; Purves et al., 2001). About 6–10% of the retinal axons in primates project to the superior colliculus *(SC)*, a complex structure in the dorsal midbrain (Grünert et al., 2021; Perry and Cowey, 1984). This circuit is crucial for controlling eye-head movements. Stimulation of the SC produces eye movements (Wurtz and Albano, 1980) and lesions of the SC produce deficits in eye gaze control (Kurtz and Butter, 1980). In some species such as mice and rabbits, most retinal axons project to the SC (Kremkow and Alonso, 2018).

A small percentage of optic tract axons terminate in the pretectum, a region adjacent to the SC. The pretectum is subdivided into five nuclei; the signals from these pretectal nuclei have an impact on pupil size, gaze and eyelid closure (Gamlin, 2006; Keane, 1990). A few thousand optic tract axons from retinal ganglion cells that are intrinsically sensitive to light (Berson et al., 2002; Dacey

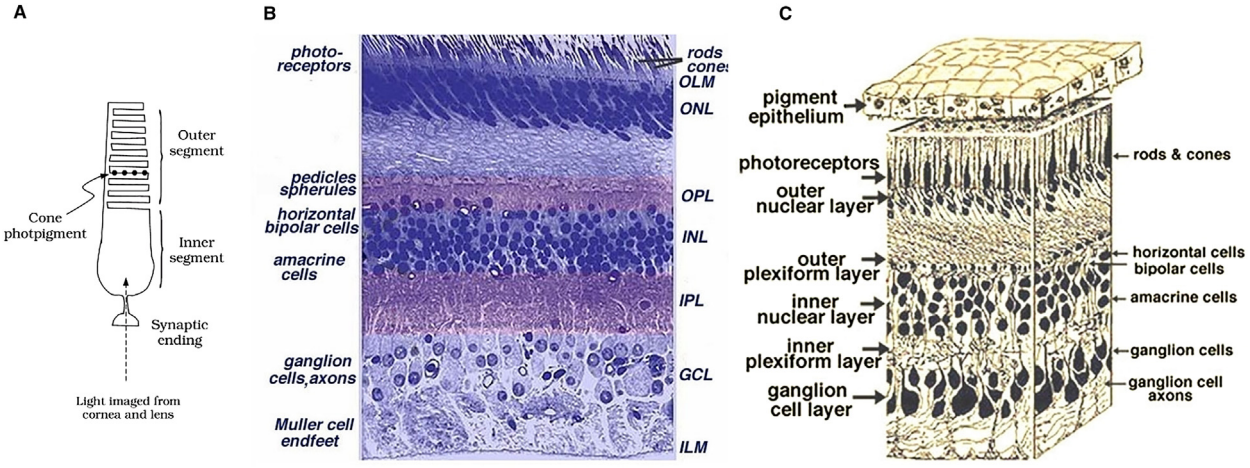

Fig. 2 (A) Schematic cone photoreceptor. (B) A light micrograph of a vertical section through the central human retina. (C) A schematic block of retina illustrating the layers and cell types. (A) After Baylor (1987). (B and C) from Kolb (2012).

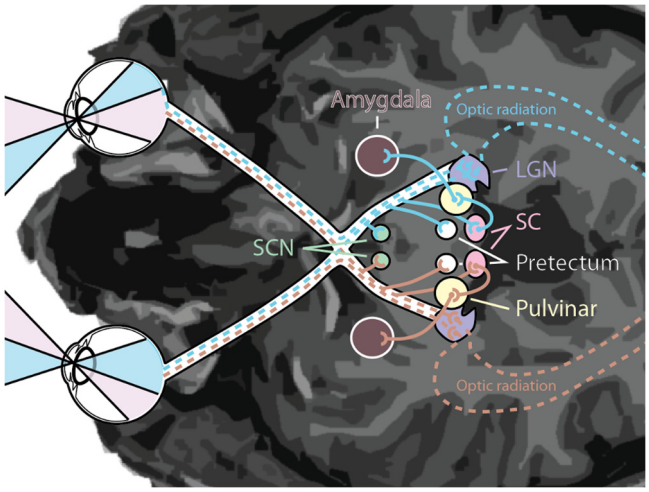

Fig. 3 The retinal ganglion cell (RGC) axons form the optic nerve. The axons from different types of RGCs have different destinations: the suprachiasmatic nucleus (SCN), just superior to the optic chiasm; the superior colliculus (SC), part of the midbrain; and the pretectum, just anterior to the superior colliculus. The superior colliculus projects anteriorly to the pulvinar, the largest thalamic nucleus, which in turn targets many other areas, including the amygdala. Each of the nuclei have numerous other inputs and outputs that are not shown. These pathways contribute to many functions, including perception, eye movements, pupil constriction, and regulation of circadian rhythms. From Winawer and Horiguchi (2017).

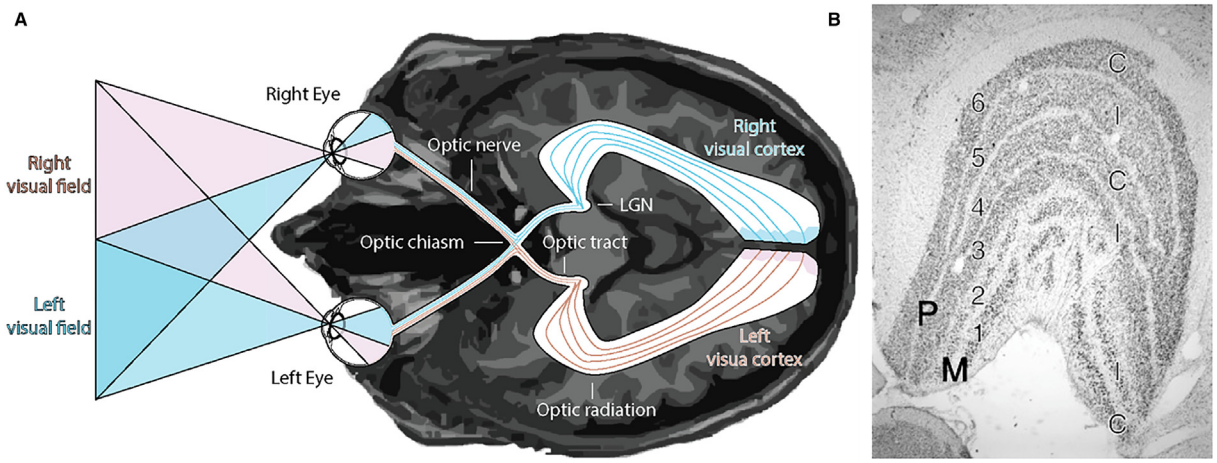

Fig. 4 (A) About 90% of fibers of the optic nerve terminate in the lateral geniculate nucleus (LGN) of the thalamus. Enroute to the LGN, at the optic chiasm, the axons from the two eyes meet. Half of the axons cross to the opposite hemisphere (hemidecussation). The inputs from the right visual field (magenta) are routed to the left hemisphere, and inputs from the left visual field (blue) are routed to the right hemisphere. Axons from the LGN comprise the optic radiation, which terminates in visual cortex. (B) The lateral geniculate nucleus is a layered structure, about the size of a walnut. The two lower layers (M, magnocellular) receive axons from the parasol ganglion cells. Layers 3–6 (P, parvocellular) receive axons from midget ganglion cells. The space between the layers is filled with very small cells (koniocellular) that receive input from the small bistratified ganglion cells. Each layer receives inputs from either the ipsilateral (I, same-side) eye or the contralateral (C, opposite-side) eye. (A) From Winawer and Horiguchi (2017).

et al., 2005) terminate in the suprachiasmatic nucleus (SCN), which is located between the optic chiasm and the hypothalamus. The SCN is an essential part of the brain's circadian rhythm system (Hastings et al., 2018).

The largest number of optic tract axons in primates—about 90% of the total—terminate in the dorsal lateral geniculate nucleus (LGN) of the thalamus (Thoreson and Dacey, 2019). The LGN has a multiple layer structure (**Fig. 4**). Axons originating in different eyes segregate into different layers, and axons from different retinal ganglion circuits are sorted into different LGN layers (Dreher et al., 1976). The axons terminate across the LGN following the spatial organization of the retina. Each LGN layer has a spatial map of half of the retina, from one eye.

The ganglion cell axons comprise only about 5% of the total number of axons that terminate in the LGN (Sherman, 2020). But they are very effective at driving cells. The other 95% of LGN inputs appear to modulate the signals created by the retinal inputs, perhaps accounting for differences in the brain's state (awake, asleep, attending, distracted).

A large group of axons exiting the LGN forms the optic radiation. Most of the fibers in this white matter tract terminate in the primary visual cortex (V1). In primates, but not all animals, lesions of the LGN or V1 lead to blindness, just as retinal lesions lead to blindness (Bullier et al., 1994). The cells in V1, like the cells in the LGN, are organized into a retinotopic map (Lister and Holmes, 1916; Wandell and Winawer, 2011); stimulation of V1 cells produces a visual sensation (Bosking et al., 2017; Brindley and Lewin, 1968).

A substantial number of axons from V1 communicate signals back to the LGN (Usrey and Alitto, 2015), and other axons transmit signals to the SC and the pulvinar, a large region within the thalamus (Sherman, 2020). Some V1 axons pass through the corpus callosum, at the midline between the two hemispheres, and terminate in V1/V2 of the opposite hemisphere.

Many V1 axons terminate in the adjacent region, V2. There is also a significant group of axons that terminate in MT/V5, a region of cortex filled with motion-responsive neurons. Many other regions of the neocortex also receive axons from V1 (Gattass et al., 1997; Ungerleider and Desimone, 1986). Lesions of these cortical regions cause specific visual defects, but not complete blindness (Bullier and Nowak, 1995).

Components

The anatomical and functional properties of the visual system components provide clues about visual processing principles. In this section, we describe properties of the main components. These are selected to provide background for the final section, when we discuss visual processing principles.

Optics

The retinal image is formed by combining the optical power of the cornea and the flexible lens. These components work together, controlled by a neural loop that controls muscles that modulate the lens shape (accommodation). The neural signals depend upon both the current image sharpness and the goals of the viewer. Focusing requires the whole system and is not explained by the individual components. Hence, a single functional goal (optical focus) is achieved by coordinating multiple components.

During the childhood years, the optical power slowly decreases and the eye size increases. The eye growth takes place at a rate that enables focus for the given optical power, a process called emmetropization (Wallman and Winawer, 2004). At any given time, the lens shape is adjusted within seconds to achieve focus for a particular object, a process called accommodation.

The amount of optical blur is commonly quantified by measuring the image produced by a point of light in the visual field (point spread function, PSF). The point can be presented with different pupil sizes, eccentricities, wavelengths, and depth compared to the accommodation plane. The size of the PSF varies with all of these experimental manipulations. For example the PSF becomes much larger with visual field eccentricity (**Fig. 5**). Software is available to simulate the PSF both with eccentricity and wavelength (Wandell et al., 2022).

The retinal image blur varies across the retina, and the blur is strongly wavelength dependent (chromatic aberration). Yet, the nervous system produces a visual percept that seems sharp over a significant portion of the visual field. The percept of a sharp scene is an inference that is created by the visual system from the retinal image.

Retinal encoding

Over most of its extent the retina is 200−300 μm thick (Lee et al., 2021) and divided into three layers (**Fig. 2**): The outer nuclear layer (ONL) containing the photoreceptors, the inner nuclear layer (INL) containing the bipolar cells, and the ganglion cell layer. But a central region of the retina, about 1.5−2 mm in diameter, is very thin and has only the photoreceptor layer: the fovea (**Fig. 6**); The bipolar neurons and ganglion cells that transmit signals from the foveal cones are piled up in the surrounding retinal region, which is particularly thick.[3]

Light is captured by the photopigment in the photoreceptor outer segments (**Fig. 2**A). There are 5−7 million cones and 100−120 million rods in each retina. There are three types of cones, differentiated in large part by the spectral sensitivity of their photopigment (cone opsins). The rods all have the same photopigment (rhodopsin).

We can infer little about the spectral energy of the retinal image from the response of a single type of photoreceptor. For that reason, we are wavelength-blind under low light conditions when only the rods are sensitive enough to respond (scotopic vision). We can discriminate between wavelengths only by comparing the responses from the three classes of cones. As a general principle, perceptual information about pattern, motion, wavelength, depth, is represented by multiple neurons (Stockman and Brainard, 2010; Wandell, 1995).

In the fovea, the cone inner segment diameters are about 2 μm. The L- and M-cones, which respond to light from about 500 to 700 nm, have a sampling density of about 100−150 cones per degree of visual angle (300 μm). This density roughly matches the best optical quality of the eye's optics in this wavelength range (50−60 cycles/deg): A very small point of light (e.g., a star) imaged at the central fovea is spread over 4−6 cones that absorb light in this wavelength band. The diameters of the cone inner segment apertures increase significantly with eccentricity, growing to 8−10 μm in the far periphery (Curcio, 1987; Scoles et al., 2014). The S-cones in primates, which absorb light in the range from 400 to 500 nm, follow a different spatial sampling pattern that is matched to the

[3]Whereas most of the retina has branching blood vessels on the inner surface of the ganglion cell layer, the very central portion of the fovea (foveola, 200 μm diameter) is avascular.

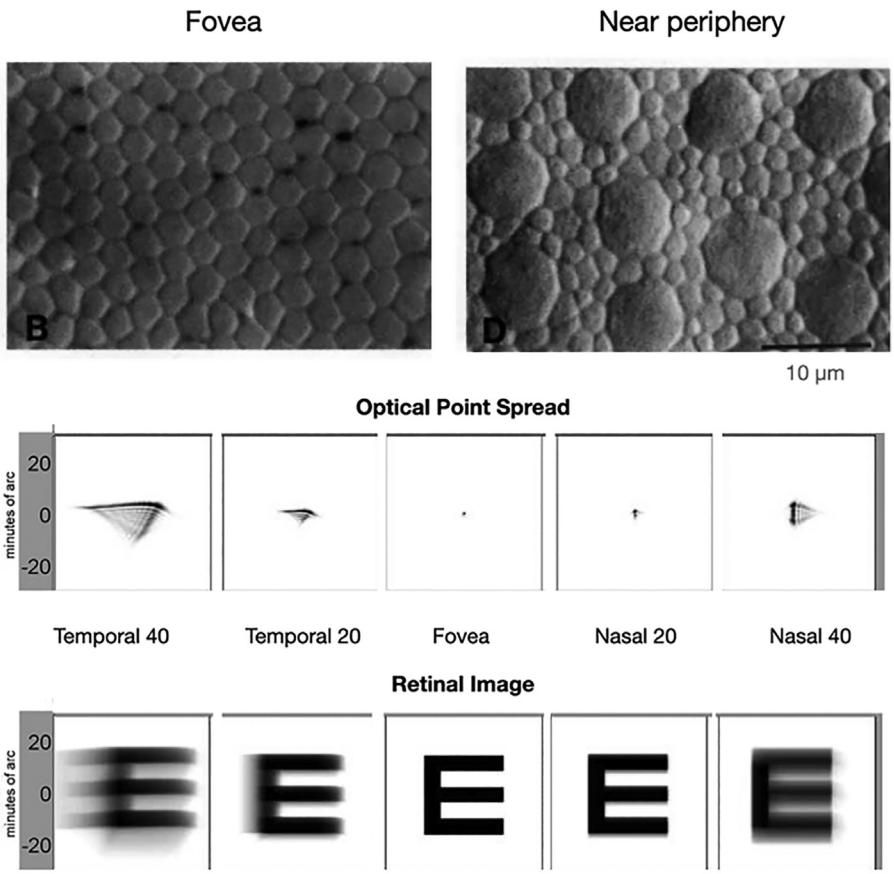

Fig. 5 (A) Photoreceptor inner segment cross-sections in the fovea and near periphery. In the fovea, there are only cones. In the near periphery the larger apertures are cones and the small apertures are rods. 10 μm is approximately 2 arcmin. (B) Simulation of retinal image PSF, and (C) convolution with letter E (size 300 arc) of a representative emmetropic subject's eye at 5 different eccentricities (left to right: temporal to nasal retina). 1 arcmin is approximately 5 μm. (A) From Curcio et al. (1990), (C) From Jaeken and Artal (2012).

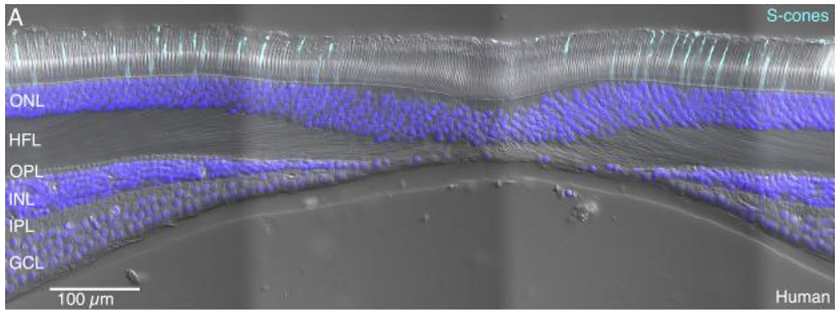

Fig. 6 A confocal image of a vertical section through the center of the fovea of a human retina. The tissue was processed with antibodies against the short-wavelength cone (S-cone) opsin (cyan) and a label for cell nuclei (blue). In the fovea the post receptoral neurons are displaced, forming a pit, and there are no S-cones. From Grünert and Martin (2020), **Fig. 4**.

optical blur in that waveband (Ahnelt et al., 1987; Martin et al., 2000) even though the light from a point is spread across multiple photoreceptors, we perceive a point, rather than a small disk. This is a perceptual inference, and the pattern of responses could have been interpreted differently.

Cone spacing imposes a maximum resolution on grating visibility. But the alignment of two lines can be judged at a much higher resolution, smaller than half the width of a cone aperture (Westheimer and McKee, 1977; Wülfing, 1892). Subjects can make very fine alignment comparisons even when the lines are moving (Fahle and Poggio, 1981). The brain makes these estimates by comparing the spatial distribution of the cone signals (Geisler, 1984; Wandell, 1995).

Retinal circuits

Photoreceptors make synaptic connections with horizontal cells, which carry signals between the cones and frequently modulate the photoreceptor-bipolar synapses (**Fig. 2**). The bipolar cell axons transmit signals to the ganglion cells. The connections between bipolar cells and ganglion cells are frequently modulated by the amacrine cells, which are present in the INL and the ganglion cell layer. The five major classes can be identified in many species, including humans (Hahn et al., 2023), but there are substantial differences in the relative number of the different cell types, and further specializations within the subtypes, in different species.

Retinal circuits are identified by tracing the specific pathways that signals traverse after they are encoded by the photoreceptors. A retinal circuit is identified by noting the pattern of connections and finding this pattern repeated across a significant extent of the retina (Rodieck, 1998). For example, a rod circuit can be identified from the connections between four cell types (**Fig. 7**, right). The rod photoreceptor synapses with a bipolar that only synapses with other rods (rod bipolar). Two amacrine cells are also part of the circuit; one modulates the bipolar cell's output and the other transmits the output to a ganglion cell[4].

The retinal ganglion cells can be further divided into about 20 different subtypes (Grünert and Martin, 2020; Kolb et al., 2020; Masland, 2012). One important criterion is where they send their axons; the axons of a specific retinal circuit typically terminate in nearby locations in the brain. The subtypes define the retinal output circuits. Five of these circuits dominate the signals from the retina to the lateral geniculate (**Fig. 7**, left).

In the primate fovea, midget ganglion cells are about 90% of the axons (Dacey, 1994). These cells sample the photoreceptor mosaic at high resolution. In the foveal region the midget circuitry, identifiable by both anatomy and function, transmits signals predominantly from a single cone (Kolb et al., 2020; Polyak, 1941). The parasol cell circuitry comprises about 5% of the foveal output. The midget and parasol circuits have center-surround organization of both on- and off-type. The center is driven by signals from the cones to the bipolars, and the surrounds are created by signals from the horizontal cells (Wool et al., 2018). The parasol cells differ from midgets in their spatial and temporal pooling of the photoreceptor signals; the parasol cells combine signals over larger regions (3−8×) than the midget cells (Dacey and Petersen, 1992).

The center-surround organization of retinal ganglion cells has played a role in many theories of visual function. These include coding schemes that reduce redundancy of the information in the cone representation (Barlow, 1961, 2001), and increase robustness to intrinsic noise (Srinivasan et al., 1982). By measuring the difference between neighboring positions in the retinal image, the system discounts the absolute level. The center-surround organization and photoreceptor adaptation both imply that image contrast, rather than absolute level, is the key variable encoded from the retinal image.

There are also retinal circuits that carry responses mainly from short-wavelength sensitive cones (S-cones). The small bistratified ganglion cells—whose dendritic arbors are much larger than the midget and comparable to the parasol—tile the retina and transmit information from the S-cones (Dacey and Lee, 1994; Field et al., 2007). Recent reports have identified other predominantly S-cone initiated circuits that combine the signals from photoreceptors spread over hundreds of microns (Patterson et al., 2020; Rhoades et al., 2019);

In addition to the multiplicity of circuits, the signals sent from different retinal regions differ. In the human fovea, there are about three ganglion cells per cone. The ratio is inverted in the periphery, where there are two cones per ganglion cell (Sjöstrand et al.,

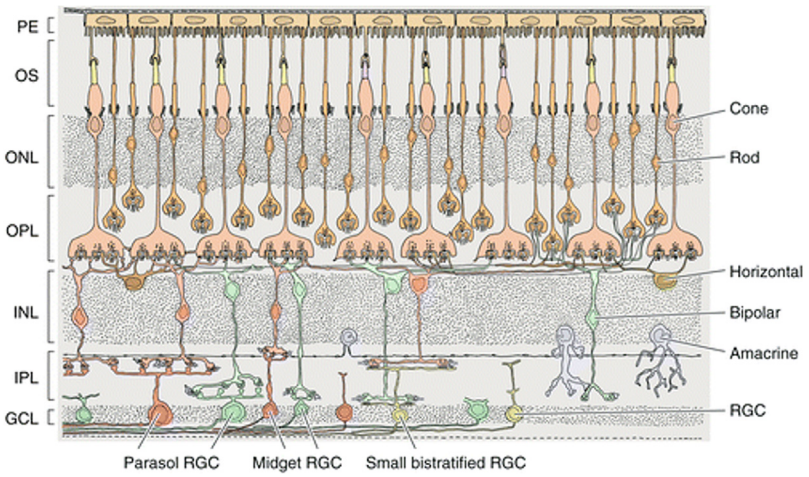

Fig. 7 The five major retinal cell classes are distinguished by morphology, connectivity, and light response properties. Photoreceptors (rods and cones), bipolars, amacrines, and RGCs make cell-type specific contacts. Five major types of RGCs that send their axons to the LGN are illustrated: the ON and OFF midget RGCs, ON and OFF parasol RGCs, and the small bistratified cells. Cells at the right show components of the rod circuitry: an A2 amacrine cell and a rod bipolar cell. Several bipolars, amacrines, and RGCs are shown with truncated and/or disconnected processes to indicate uncertainty about their morphology and connectivity. Modified with permission from Rodieck (1998); From Field and Chichilnisky (2007).

[4]The same ganglion cell can also be driven by a separate circuit that is initiated by the cones.

1999). The relative proportions of the different circuit types also change: the percentage of midgets declines to 40−45%, while parasols increase to 20%, and small bistratified increases to 10% (Dacey, 1994).

The properties of individual cells also vary across from fovea to periphery. For instance, the size of photoreceptor inner segments and the dendritic arbors of most cell types tend to increase with eccentricity. As a result, circuits are primarily identified based on their connection patterns rather than the absolute size of the cells. The response dynamics are also heterogeneous; photoreceptor responses are slower in the fovea than the periphery (Sinha et al., 2017) and the dynamics varies between retinal circuits (Kaplan and Benardete, 2001). Moreover, even though a circuit is present in multiple retinal locations, it is not necessary for it to be uniformly distributed throughout. The central fovea lacks rods, leading to the absence of rod circuitry in this particular region. At each location, the retinal output consists of multiple, parallel circuits whose functional properties provide complementary information about the responses of the photoreceptors (Soto et al., 2020; Thoreson and Dacey, 2019). Thus, beginning in the retina there are large spatial and temporal nonuniformities in the encoded signal.

The nonuniformities across the retina are not normally noticed in vision, begging the question of how the percept of a single, high resolution scene is assembled from such disparate components (Burge et al., 2019; Burge and Dyer, 2023). How the visual system integrates this array of asynchronous signals to form a coherent percept is an important challenge.

The signals within the retina operate through at least two distinct mechanisms. Firstly, cells communicate via chemical synapses, releasing neurotransmitters. Additionally, cells establish electrical junctions with other cells. The effectiveness of these gap junctions is influenced by neuromodulators present in the extracellular space. The majority of retinal signals are graded voltages, with only the retinal ganglion cells transmitting action potentials along their axons[5] (Bloomfield and Völgyi, 2009; Söhl et al., 2005).

The retina also contains three types of glial cells: microglia and two types of macroglia, astrocytes and Müller cells (Reichenbach and Bringmann, 2020; Vecino et al., 2016). These cells play a role during development, damage, and synaptic signaling. Our understanding of the retinal circuitry will be incomplete until we understand the glial cell functions.

Eye movements

The fovea is an important specialization in the primate retina. Other animals have specializations in the central field of view, but the primate fovea has its own specific features (Bringmann et al., 2018; Tuten and Harmening, 2021). For example, the primate visual system has a system for controlling head and eye movements to encode a region of interest on the high resolution fovea (Ibbotson and Krekelberg, 2011; Wurtz, 2008).

The eye movement system is extremely active, in the sense that eye movements typically occur a few times per second (more than 200,000 times per day). Some amount of retinal image motion is required for sustained perception; stabilized images—such as the shadows of the blood vessels—are not visible (Mark, 2014). The small retinal motion due to fixational eye movements are a major source of image motion (Engbert et al., 2011; Reichle et al., 2003).

Distinguishing the retinal motion caused by eye movements from motion in the scene is an important task for visual processing. The problem is partly solved by reducing awareness of visual stimuli during large saccadic movements, a phenomenon called saccadic suppression (Binda and Morrone, 2018; Dodge, 1900; Krekelberg, 2010). We have little awareness of this suppression because visual processing combines retinal signals before, during, and after the saccade into a single, stable percept.

The neural systems that direct larger eye movements (pursuit and saccades) are also essential for vision (Kowler et al., 2019; Kümmerer and Bethge, 2023; Robinson, 2022). These systems make a decision about where to locate the high resolution fovea. This implies that eye movement systems combine information from vision and cognition. The eye movement decision depends both on the scene contents and the person's goals. In some cases the decision is conscious, and other cases the decision is involuntary or subconscious.

For thirty years investigators have developed models to predict the likely eye movement path when free-viewing an image—that is, viewing without an experimenter directed goal (Itti et al., 1998). This work has often been part of models of visual saliency and attention (Itti and Koch, 2001). The field has evolved from an initial framing of saliency in terms of the image features (e.g., contrast, edges) to models based on high level (object) features (Kümmerer et al., 2022; Kümmerer and Bethge, 2023). The success of the newer models support the long-held view that the visual system has methods that link objects observed before and after a saccadic eye movement (Dowd and Golomb, 2020; Treisman and Gelade, 1980).

Some linking information can be gleaned from the image itself. In addition, the motor centers that direct the eye movements send a copy of the saccadic command—a corollary discharge—to the visual pathways (Subramanian et al., 2019; Wurtz and Sommer, 2004). The eye movement control signals can also be helpful in linking. Information sharing may be a general principle. It seems likely that when a neural circuit makes a decision, the information is sent to many other neural structures.

Retino-geniculo-cortical pathway

The axons from the two eyes and different retinal circuits terminate in different layers of the LGN (**Fig. 4**). The primate LGN (Dreher et al., 1976) has two layers with large cells (magnocellular, parasol cells) and four layers with small cells (parvocellular, midget cells). The axons from these LGN layers terminate in distinct layers (4Cα, 4Cβ) of the primary visual cortex (Hubel and Wiesel, 1972). The axons from small bistratified retinal ganglion cells project to thin layers ventral to (below) each of the midget and parasol layers (Roy et al., 2009). These are called the *koniocellular layers* (Casagrande et al., 2007; Hendry and Reid, 2000; Hendry

[5]Aside from certain types of amacrine cells.

and Yoshioka, 1994; Vanni et al., 2020). The axons from the koniocellular layers terminate in the upper layers 2 and 3 of primary visual cortex. The three pathways are often labeled by the LGN cell types: magnocellular (M−, (parasol, magnocellular, 4Cα)), parvocellular (P−, (midget, parvocellular, 4Cβ)), and koniocellular (K−, small bistratified, koniocellular, 2/3) pathways.[6]

Axons are not organized retinotopically within the optic nerve (Fitzgibbon and Taylor, 1996). Upon arrival in the LGN, they form connections so that there is a retinotopic map within each layer from one eye (Kremkow and Alonso, 2018). Within these maps, cell counts reveal an increasing emphasis on the foveal representation in the LGN. The ratio of RGC to LGN cells varies from fovea to periphery, with a ratio of 1 RGC to 3 LGN cells in the fovea but 1:1 in the periphery (Schein, 1988).

The optic tract axons terminating in the LGN connect to cells that, in turn, send their axons to the visual cortex. A large number of axons from regions other than the retina also terminate in the LGN. The signals from these axons appear to modulate the retinal signals en route to V1. The implementation of these modulations is an interesting topic that includes speculations of gating which signals are transmitted, managing the graceful degradation of signals, and temporal decorrelation (Weyand, 2016).

The LGN is one of many locations in the visual pathways containing multiple feedforward circuits. The LGN also receives a large set of axons from V1 (Usrey and Alitto, 2015); this may substitute for the absence of retinal feedback. The anatomy suggests that the LGN is a place where retinal circuits are modulated by signals from other brain regions that reflect other behavioral states and goals.

Geniculo-cortical projections

The LGN axons principally terminate in V1 in an orderly way that preserves the retinotopic organization. In humans the foveal representation is located in the posterior occipital cortex, often just lateral to the occipital pole. Signals from increasingly peripheral retina arrive at V1 locations at increasingly anterior positions near the calcarine cortex.

Another group of LGN axons terminates in a distinct region of the visual cortex (MT/V5) (Sincich et al., 2004). This cortical area contains neurons that are very responsive to moving stimuli (Albright, 1984). An even smaller group of LGN axons, primarily from the koniocellular layers, terminate in V2 (Bullier and Kennedy, 1983).

The amount of cortex that responds to one degree of the visual field is called the cortical magnification factor (deg/mm). This value varies dramatically with eccentricity. In the central fovea, 1 deg of the visual field excites approximately 1 cm of cortex; at 5 deg eccentricity 1 deg of the visual field excites only 2 mm of cortex (Dougherty et al., 2003; Harvey and Dumoulin, 2011). The reduction in the cortical extent—and thus number of neurons—representing each degree of the visual field is qualitatively similar to the reduced number of cones and retinal ganglion cells in the retina.

There are about 1.2−1.5 million retinal ganglion cell axons; LGN neuron counts suggest about 2.5−3.5 million (Finlay et al., 2014); V1 neuron counts range from 180 to 600 million (Kelly and Hawken, 2017; Suner and Rakic, 1996; Vanni et al., 2020). The V1 neural circuitry is a massive increase of the number of cells compared to the retina and LGN.

Given this expansion, it is clear that V1 includes cell types and circuits that differ from the retina-LGN inputs. More than 60 different types of neurons have been reported already, based on single-cell RNA sequencing (Wei et al., 2022) and single-nucleus RNA sequencing (Hodge et al., 2019). Given the history of cell type discovery in the retina, which progressed over a period of 50 years, we are at the early stages in understanding cortical cell types. It is already clear, however, that there are many different cortical cell types that differ in their typical laminar location, excitatory and inhibitory properties. Our ability to identify neural circuit mosaics in the primate cortex is not yet as advanced as the ability to find mosaics in the retina. Many limitations make it difficult to identify circuits that tile the visual field with common connections and functional properties.

V1 functional responses

The stimulus-driven responses of LGN neurons are similar to the responses of their retinal ganglion cell inputs. The responses of V1 neurons, however, include many properties that are not found in retina or LGN (Hubel and Wiesel, 1968, 1977).

There are three prominent new functional properties in V1.

1. *Binocular*. The LGN inputs to V1 are segregated by eye of origin. The circuitry within V1 combines the signals from the two eyes into neurons that respond to corresponding locations in the visual field from either eye.
2. *Oriented*. The receptive fields of retinal ganglion cells and LGN neurons are roughly circularly symmetric, with modest but systematic orientation preferences (Leventhal and Schall, 1983). Many neurons in primate V1 have receptive fields that show strong orientation preferences, and these neurons are arranged in an orderly progression so that small changes in position produce neurons with small changes in preferred orientation (Hubel and Wiesel, 1977).
3. *Direction-selective*. Some neurons in V1 respond preferentially to patterns moving in a specific direction.

Understanding how the cortical circuits are implemented is an enormous task and many of the questions we might ask are beyond the reach of current technology. "All evidence points to a mixing of M, P, and K pathways within the primary visual cortex to give rise to a new set of pathways that project … to higher visual cortical areas (Callaway, 2005)."

Functional magnetic resonance imaging (fMRI) in the living human brain is an indirect measurement of neural activity. The measure depends on the average metabolic activity across hundreds of thousands of neurons, filtered through the slow temporal response of the vasculature. The fMRI measurements can be meaningfully compared to some anatomical and electrophysiological measures. For example, fMRI has provided guidance about the size, retinotopic organization and population responses in V1 and

[6]The reversal of the letters for midget/parasol and parvocellular/magnocellular is unfortunate.

other cortical regions (Wandell et al., 2007; Wandell and Winawer, 2011). As the resolution of MR scanners and data analysis methods have advanced, a better understanding of how to connect the fMRI and electrophysiological measures is emerging (Logothetis and Wandell, 2004).

V1 axons

Many axons in V1 make local connections within the cortex. Other axons enter the white matter and terminate in remote targets in the cortex or thalamus. The axons that enter the white matter form bundles (thousands of axons or more) that carry both feedforward and feedback signals. In the human brain the white matter volume is roughly equal to the cortical gray matter volume. This ratio is much smaller in many other species (Zhang and Sejnowski, 2000).

The largest white matter tract is the corpus callosum, which transmits information between the two hemispheres (200−300 million axons). There are published atlases describing the likely position and size of about twenty major tracts (Yeatman et al., 2012; Zhang et al., 2018). There are also many relatively short tracts (U-fibers) that connect nearby regions of the cortex (Schüz and Braitenberg, 2002). Finally, there are many axons within the gray matter itself. C.F. Stevens estimated that each cubic millimeter of cortex contains a length of 3 km of fibers that interconnect these neurons (Stevens, 1994).

The connections between V1 and V2, a region that surrounds V1, are short-range. These connections are asymmetric: V1 axons terminate at the input layers of V2, and V2 axons terminate in feedback layers of V1. This anatomical difference is functionally significant: silencing visually driven activity in V1 silences V2 responses, but not the reverse (Bullier et al., 1994).

Axons from V1 also make a direct connection with the motion-responsive cortex (V5), a small region several centimeters away from V1 on the lateral cortical surface. As methods for detecting axonal projections have become more sensitive, investigators have identified additional projections (Schmidt et al., 2018).

V1 axons also send feedback signals to the LGN and pulvinar, both in the thalamus (Sherman, 2020; Shipp, 2003). These axons arise in part from layer 6 of V1, and the axons in different subdivisions of layer 6 project to the parvocellular and magnocellular layers (Briggs et al., 2016; Lund et al., 1975).

There are very different perceptual consequences of lesioning V1 compared to other cortical regions. In primates a lesion of the retina, LGN or V1 leads to blindness; but a lesion of V2 or other regions does not (Bullier et al., 1996; Merigan et al., 1993). Lesions outside of V1 produce a variety of perceptual deficits with characteristics that depend on the lesion location and can be hard to quantify (Tong, 2003).

Anatomical measurements in primates have identified more than 1600 white matter pathways between cortical regions, a subset of the total number and estimated that about two-thirds of all the potential cortico-cortical connections exist (Markov et al., 2014). Diffusion MRI and tractography in living humans can now identify the larger tracts that are known to be present (Rokem et al., 2017; Wandell, 2016).

Cortical layers

The human cortex is a continuous sheet with many folds. In many parts of the sheet, the cortex is divided into six layers that were first visualized with the unaided eye (Baillarger, 1840). This observation has been subsequently confirmed by increasingly sophisticated methods (Bernard et al., 2012; Wei et al., 2022), with some deviations (Barbas, 2015). With advances in staining and transcriptional methods, cell types with different body shapes, and dendritic arbors, have been classified from the superficial layer 1 to the cortex/white matter boundary at layer 6 (Palomero-Gallagher and Zilles, 2019; Wagstyl et al., 2020).

In much of the visual cortex the cortical layers typically have anatomical properties that suggest their roles. Cells originating from different types of retinal ganglion cells (parasol and midget) synapse into slightly different levels of layer 4. Cells carrying a strong signal from the short-wavelength (blue) cones, largely terminate in layers 2 and 3.

About half of the pyramidal cell axons connect within V1. For example, axons from cells in layer 4 terminate in the superficial layers 2/3, which contain a large number of pyramidal cells. Other axons terminate within layers 5 and 6. Nearly half of the pyramidal cell axons have a branch that enters the white matter, forming long-range projections to other parts of the cortex (Callaway and Wiser, 1996; Vanni et al., 2020) or thalamus. For example, the axons in layers 5 and 6 frequently terminate in the thalamus (Usrey and Alitto, 2015).

Recent advances in functional MRI make it possible to measure signals that appear to arise preferentially from the neurons in different layers (Finn et al., 2021; Merriam and Kay, 2022; Self et al., 2019). The ability to resolve fMRI signals from specific layers depends in part on the spatial distribution of the vasculature.

There is ongoing work to understand whether the layer characteristics in the visual cortex generalize across species and to other regions of the cortex (Barbas, 2015; Rockland, 2019). Some investigators have argued for the existence of a stereotypical architecture across the layers—called a canonical cortical circuit (Douglas and Martin, 2004). These authors attribute a goal to at least some of the neurons in the superficial layers, suggesting they "cooperate to explore all possible interpretations of different cortical input and cooperatively select an interpretation consistent with their various cortical and subcortical inputs." The relationship to Helmholtz's unconscious inference, but at the cellular level, is clear.

V1 columns

Neurons in the different layers often form stereotypical connections with other neurons just above or below. This pattern of connections is called a cortical column, and it is an organizing anatomical principle (Mountcastle, 1997). Anatomical columns are widely identifiable, but the functional role of a column is not always certain (Horton and Adams, 2005).

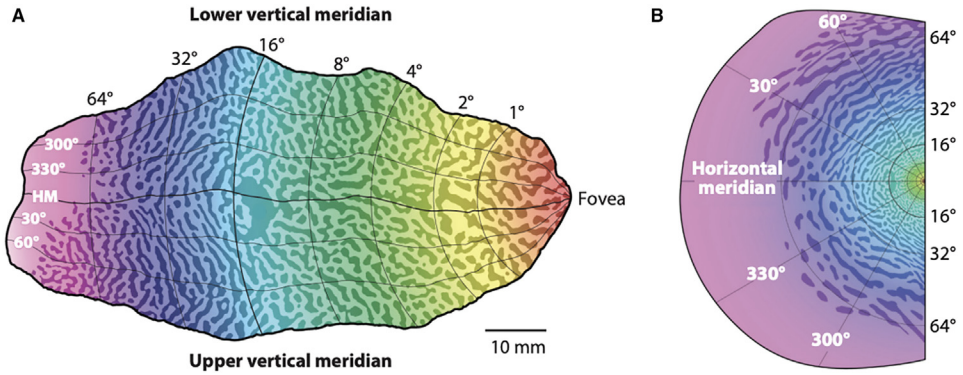

Fig. 8 (A) Human V1 ocular dominance regions (lighter vs. darker) shown on a flattened representation of V1. The color gradient represents the eccentricity map. (B) The ocular dominance superimposed on the visual field representation. The ocular dominance bands rotate around the center of vision and are perpendicular to the vertical meridian representation at the V1/V2 border. From Kremkow and Alonso (2018).

The inputs from the two eyes form one of the clearest examples of a cortical column (Kremkow and Alonso, 2018) (**Fig. 8**). The LGN axons from different eyes terminate in layer 4C, with axons from each eye dominating the targeted region in alternation. The width of these ocular dominance columns ranges from about 0.6 mm near the fovea to 1.5 mm in the periphery.

Cortical maps

In many cases the axonal projections between cortical regions preserve the retinotopic organization. The axonal arbors of cells usually make dense contact with nearby neurons, so it appears that preserving retinotopy to facilitate spatially local processing is another fundamental principle that is repeated in many parts of the visual cortex.

The existence of multiple retinotopic maps in the cortex of animal models was established by a series of challenging anatomical and electrophysiological experiments, likened to "a dismaying exercise in tedium, like trying to cut the back lawn with a pair of nail scissors (Hubel and Wiesel, 2004)." Functional MRI enabled much more efficient measurements of these maps (**Fig. 9**) in the human and macaque cortex (Brewer et al., 2002; Engel et al., 1994, 1997; Kolster et al., 2009; Tootell et al., 1996). The maps in human and macaque are similar, but not precisely the same (Brewer et al., 2002; Wandell et al., 2007, p. 375).

The large number of maps provoked the question of the relationship between the maps. Several models have been proposed, including a hierarchical structure (Felleman and Van Essen, 1991), with maps grouped into a dorsal and ventral stream (Mishkin et al., 1983; Ungerleider and Mishkin, 1982; Zeki, 2015), or perhaps a dorsal, ventral and lateral stream (Battelli et al., 2007; Pitcher and Ungerleider, 2021; Weiner and Gomez, 2021). It has also been noted that the maps group into small clusters that share a common eccentricity map (Kolster et al., 2009; Wandell et al., 2005; Wandell and Winawer, 2011). These clusters may be another organizing principle.

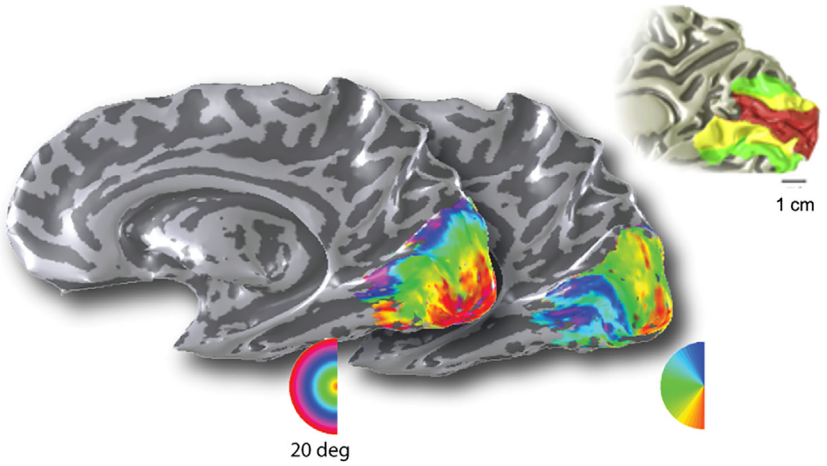

Fig. 9 FMRI estimates of the V1, V2 and V3 maps in a single human subject. Posterior occipital lobe has an eccentricity map that extends from the occipital pole forward. The foveal representation is magnified; notice the second foveal representation on the ventral surface. The eccentricity map is divided into V1, V2 and V3 by measuring the angle representations. Upper inset: V1 (red) is a hemifield in the calcarine sulcus; V2 (yellow) and V3 (green) surround V1.

There are significant differences between the functional responses measured in different maps. These are clear using either single unit electrophysiology or functional MRI (Gattass et al., 2005; Greenlee and Tse, 2008; Maunsell and Newsome, 1987). One early hypothesis for this difference is that different portions of the cortex receive different inputs. An important hypothesis was that the dorsal (top) stream received mainly magnocellular (fast, low-resolution) signals and the ventral stream received parvocellular (slow, high-resolution) signals (Livingstone and Hubel, 1988).

However, subsequent tracer studies in macaques revealed that the ventral stream receives input mainly from the central (foveal) region of the retina, while the dorsal stream receives input mostly from the peripheral areas (Baizer et al., 1991). This suggests that the dominance of magnocellular signals in the dorsal stream can be explained by its relative emphasis on processing information from the periphery, which has a larger ratio of magnocellular to parvocellular circuits, and the main difference seems to be which portion of the retina is delivering the signals.

Cortical areas

The definition of a cortical visual field map is straightforward: neurons within a region have relatively localized receptive fields, and the positions of the neurons match the relative position of the receptive field centers.

A second term, cortical area, is also used widely. A cortical area is "a distinctive region of cortex that differs reliably from neighboring areas in one or more neurobiological properties from four basic categories: function, architecture, connectivity, and/or topographic organization (Van Essen and Glasser, 2018)." Function refers to the area's specialized role, such as processing visual information in the primary visual cortex. The term "architecture" encompasses the arrangement of neurons, including their density and morphology. Connectivity describes the area's communication pathways with other brain regions, while topographic organization refers to the presence of map-like representations of the sensory or motor world. In the visual cortex, topography means a retinotopic map.

These four criteria provide a valuable framework, but their application is not straightforward because the criteria may conflict with each other (Wandell et al., 2005). For example, a functionally distinct region might form similar connections to adjacent regions with different functional properties. Hence, the determination that a region is a cortical area is a judgment.

Despite this limitation, the notion of cortical area is useful for regions that do not have clear maps. The face-responsive region in the human fusiform gyrus is a good example. Measured with fMRI, this cortical region has a specific functional response (Kanwisher et al., 1997; Puce et al., 1995), and analyzed in postmortem tissue it has a distinct cytoarchitecture (Weiner et al., 2017). There is no clear retinotopic map. Hence, this region is called the "fusiform face area." Similar to the discovery that there are multiple visual field maps in the occipital lobe, detailed measurements in human and animal models indicate that face-responsive cortical processing is carried out by a network of multiple interconnected areas rather than a single region (Chen et al., 2023; Freiwald, 2020).

Cortex and eye movements

The great benefit of integrating data from multiple eye movements is that the viewer creates a single, high-resolution internal representation with a field of view that extends far beyond the small foveal field of view (Stone et al., 2003). The question of how the visual system integrates information across eye movements and channels is a key question that must be addressed to understand visual processing principles.

Measurements of functional MRI signals in humans suggest that information about the direction of gaze and eye movements is present in the first few retinotopic maps (V1, V2, V3). One experiment matched the retinal image motion between conditions when the eye moved or the eye was stable. The response to stimuli in these maps differed, showing that the response depends on eye movement, not just the retinal stimulus (Nau et al., 2018). A second study showed that the relative amplitude of fMRI responses in V1 can vary by as much as a factor of two, depending on the direction of gaze (Merriam et al., 2013).

In primates the direction of gaze is also a social signal[7] (Ethofer et al., 2011; Gobel et al., 2015).

Functional specializations in cortex

There are a number of measurements suggesting that there are small regions with a high degree of functional specialization in the cortex. Electrophysiological recordings of single neurons in non-human primates revealed clusters of neurons that appear to be particularly responsive to specific classes of stimuli, such as faces (Gross, 1992), and similar responsiveness to faces and words was seen in local field potentials in human patients (Allison et al., 1994; Nobre et al., 1994) (**Fig. 10**).

The behavioral consequences of cortical lesions, caused by disease in humans or by experiment in non-human primates, are associated with impaired performance on face recognition, color perception, and reading (Boeri and Salmaggi, 1994; Meadows, 1974a,b; Wandell, 2011; Wandell et al., 2012). Functional MRI measures, building on these neurological and related PET findings, have identified many small cortical regions adjacent to the retinotopic maps that respond more strongly to one class of stimuli (e.g., faces, colored patterns) than other classes (Grill-Spector and Weiner, 2014). In some cases, the neuroimaging activations roughly align with the deficits from cortical lesions (Bouvier and Engel, 2006). The functional localization approach has also motivated the search for small specialized cortical regions that are identified using electrophysiology in macaque (Conway, 2018; Hesse and Tsao, 2020).

[7]Also dogs and cats (Koyasu et al., 2020).

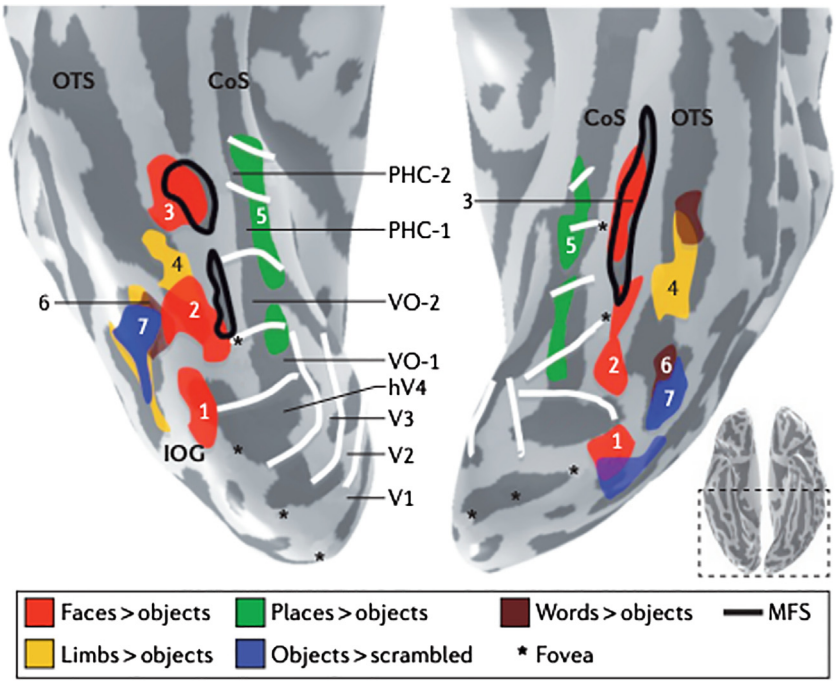

Fig. 10 Functional MRI measurements have been used to identify small cortical regions that respond preferentially to specific stimulus classes: (faces, red), (places, green), (words, brown), (limbs, yellow) and (objects, blue). Locations are shown on the inflated hemispheres of a representative subject. These regions have a consistent spatial organization on the inferotemporal cortex, both with respect to one another, the sulcal pattern and the visual field maps. For example, place regions are medial to face regions, and limb regions separate two of the face regions. From Grill-Spector and Weiner (2014).

The presence of patches of cortical regions that respond substantially more to one type of stimulus compared to others does not determine a visual processing algorithm. The cause of this stimulus tuning in a patch surely depends in part on processing carried out by other neural components. For example, the responses of face-selective neurons must depend on processing in the retina and several early retinotopic maps. Computational hypotheses are needed to explain how the stimulus tuning arises. The hope is that once such a region is identified, we might measure the components connected to that region and use the full set of measurements to develop a model of the processing pipeline.

Cellular signaling

For many years the electrophysiological literature reported mainly about action potentials. These are very important because all cortical regions communicate to distant parts of the brain via action potentials in the white matter. For local communication, the nervous system has multiple methods with different dynamics and spatial distribution.

One method, direct electrical coupling via gap junctions, is extremely fast and localized. Another method, chemical transmission, can be subdivided in various ways. One division is between "wiring transmission" and "volume transmission" (Agnati et al., 2010). The first refers to signaling with delimited physical boundaries of the synapses and gap junctions. The second refers to signals that diffuse through the extracellular space. Neuromodulators, such as dopamine, are volume transmitters. Their presynaptic release is followed by diffusion that activates receptors of many target cells (Liu et al., 2021).

An additional division is between different types of synaptic transmission. Neurotransmitters can act directly on channels, being direct and rapid (ionotropic). Or their action can be mediated by G protein-coupled pathways that include a variety of kinetics and characteristics (metabotropic). Some neurotransmitters, such as glutamate, can act through both mechanisms (Reiner and Levitz, 2018).

Virtually all of the work we describe here concerns neurons, which comprise about half of the cells in the human cortex. Glia make up the other half (von Bartheld et al., 2016). The glial cells play an important role, and new discoveries about their function are reported monthly. Astrocytes are important for synaptic transmission (Araque et al., 1999; Perea et al., 2009). Oligodendrocytes play a critical role in neural transmission and their impact can even be assessed in learning and memory tasks (Fields, 2015; Mount and Monje, 2017; Munyeshyaka and Fields, 2022). Glial cells also transmit signals and their signals are fully integrated into the neural network (Verkhratsky and Nedergaard, 2018). Finally, the axons in the white matter communicate with glia—particularly oligodendrocytes that form the myelin sheath—via neurotransmitter release. This communication is likely to impact neural transmission (Habermacher et al., 2019; Talidou et al., 2022) Our understanding of visual processing will be incomplete until we understand the impact of the full complement of cellular signaling mechanisms, including both neural and glial functions.

Historically, reporting on the firing rate of individual neurons that were "well and truly" isolated was considered the ideal approach for assessing functional responses. In recent years, there has been broader acceptance of other neural signals. It is now feasible, and common, to record electrical potentials from many neurons at once, enabling assessments of population level behavior that cannot be inferred from single neuron data. It is also now common to measure aspects of circuit behavior other than the spike rate of individual neurons, including calcium levels, membrane voltages, and metabolic rates. For many years these signals were dismissed, despite pleas to take them seriously (Bullock, 1997). Understanding the relationship between these measures, and accounting for their differences, may provide a more complete measurement of neural activity and visual processing.

Processing principles

Visual neuroscience is awash with data; there is no indication that the data acquisition rate will slow soon. There are many computational methods for analyzing data—mainly summarizing and simplifying. These methods draw on the foundations of linear algebra, such as basis change (e.g., Fourier, wavelets), dimensionality reduction (e.g., principal component analysis), and the foundations of statistics (Gaussian and Poisson noise, Bayesian inference). Important as they are, these tools are not theoretical ideas about visual processing, any more than Shannon's information theory is a model of real television signals.

In defining how visual processing principles are implemented, we account for the measured anatomical architecture and functional signals in a visual system. The principles should explain the processing of these signals in the system, and we aspire to link these anatomical structures and functional signals to visual performance and perception. Throughout, we must consider the anatomical organization to be important, while still recognizing that it does not specify the functional responses. Functional properties, such as how cones adapt to different light levels and retinal ganglion cells respond to spatial patterns, cannot be deduced from anatomy alone.

Secure theoretical models that link neural measurements to behavior or conscious experience are rare. One widely accepted principle formulated by Brindley is this: When two stimuli produce the same neural response, at a neural bottleneck, the stimuli must appear the same (Brindley, 1970). Color matching is an example: having three types of cone photoreceptors is a bottleneck for discriminating light spectra (Stockman and Brainard, 2010; Wandell and Brainard, 2021). Brindley referred to experiments as "type A" if they assess sets of stimuli that are not distinguishable. Everything else is "type B." Threshold measurements are appropriate for type A analyses, but in most cases the neural bottleneck is not known (Cottaris et al., 2020).

There is much we can learn about vision through the Brindley's type A experiments, but there are also topics that do not fall into this approach. For example, establishing that there is no difference between two stimuli falls short of the goal of explaining the appearance of the stimuli. We have only an inkling of a secure theory that characterizes the network of visual processing and connects these neural signals to perceptual experience. Developing a powerful framework will require new ideas. Here, we describe important ideas that are helpful for advancing this goal.

Receptive fields

One important type of measurement is to characterize the properties of individual neurons. In most parts of the brain, it is not yet possible to measure the many thousands of neural and glial inputs that determine a neuron's response. It has become common, therefore, to build response models with respect to carefully controlled input stimuli. These are called input-referred models in other fields, and they are called receptive fields in visual neuroscience.

Initially, receptive fields served to characterize the visual field locations where a stimulus influenced the neuron's activity. The initial qualitative measurements were followed by quantitative linear models that predicted the response as a weighted space-time sum of the stimulus contrast. Linear models worked well for certain retinal (Enroth-Cugell et al., 1983) and V1 circuits (Movshon et al., 1978) over small contrast ranges. As the contrast increases, a static nonlinearity would be applied. The failure of linear models in predicting other circuit responses, even for low contrast stimuli, led to the discovery of functional cell types that corresponded to anatomical cell types in the retina (Enroth-Cugell and Robson, 1984) and new circuits in V1 (Rust et al., 2005).

In addition to characterizing individual neurons, measurements revealed neurons arranged in orderly maps of stimulus specific stimulus features. In V1 there are systematic representations of the orientation of the local contrast (Hubel and Wiesel, 1974). In MT/V5, an area of cortex with many motion responsive cells, there is a map of the motion direction (Albright, 1984), a superimposed map relating to binocular disparity (DeAngelis and Newsome, 1999) and a retinotopic map (Kolster et al., 2010). The discovery of receptive fields organized into feature maps suggests that spatial proximity of neurons is an important general requirement for visual processing.

Redundancy

For a period of time removing redundancy in the neural signal was considered to be a central visual processing principle. One motivation was asking how signals from approximately 5 million cones could be carried by only 1 million optic nerve fibers. Making the image representation efficient gave rise to an interesting set of theoretical ideas directed at explaining the retinal encoding (Atick, 1992; Atick et al., 1992; Barlow, 1961).

We have learned, however, that in the fovea there are multiple retinal ganglion cells per cone, and for each region of the visual field there are far more V1 neurons than retinal ganglion cells or LGN cells. The principle of removing redundancy has been applied to other domains. One idea is a search for how the visual system might be structured to interpret the image, given natural scene statistics (Simoncelli and Olshausen, 2001). Other ideas include the value of redundancy reduction in noisy systems, and limiting signals to reduce energy consumption (Barlow, 2001; Barlow et al., 2009; Laughlin, 2011; Lennie, 2003). For these reasons, the principle of efficient representations remains important.

Maps and areas

The existence of multiple cortical maps and areas provoked the question of why there are so many. One explanation for a multiplicity of areas goes directly to the heart of brain function:

Zeki (1990, 2005), Kanwisher (2010) and Ratan Murty et al. (2021) believe that these measurements vindicate a processing principle of functional specialization. They argue that areas exist to complete the calculation of specific, important attributes such as color, motion and features such as faces, objects, and limbs. They see the discovery of multiple areas as resolving the Fluorens and Gall debate (Pearce, 2009): Does the brain function as (a) an integrated whole, or (b) a set of discrete, specialized circuits?

At this time there can be no serious debate as to whether brain computation is distributed or localized: it is both. In support of localization, disrupting the visual cortex does not render us deaf and disrupting the motor cortex does not render us blind. In support of distributed functionality, it is clear that reaching behavior requires circuits that coordinate distributed activity between vision and motor systems. At finer scale, portions of the visual circuitry (V1) are used for all visual judgments while other circuits may be local and specialized (Fusiform face area). The modern formulation is that visual signals pass through a series of general components, and then additional components that become increasingly specialized (Sejnowski et al., 1988). In this formulation, the specializations are for perceptual features, such as color, motion, faces, body parts, objects, outdoor spaces and food.

Barlow offered a computational perspective that differs in kind from localization (Barlow, 1986). He observed that when using computers, it is possible to compare values across a very large amount of memory (address range). But in the brain, comparisons of the response of a neuron are limited to a relatively short distance. A neuron's activity, he argued, can be compared with several thousand nearby neurons, whereas a value in computer memory can be compared to values in a memory many orders of magnitude larger. He suggested that the brain creates multiple areas to extend the ability to make comparisons, compensating for this addressability limitation.

As an example, consider how one might ask whether a line is straight. To do this, we need to judge the orientation as we traverse the line. If the line is long, its endpoints will cause activity at widely separated retinotopic positions. It would be useful to have a representation that places information about line segment orientations in close proximity.

An example is visual area (V5/MT), where neurons are organized into a map in part based on the direction of stimulus motion and in part based on binocular disparity (**Fig. 11**). This makes it possible for a neuron connected to a small region of V5/MT to compare the response level between nearby neurons with a range of preferred directions of motion. The result of this comparison information might be contained in either feedback or feedforward signals sent to other parts of the cortex where perceptions are assembled. Barlow's idea is a computational principle. It suggests that the receptive field properties are not tightly connected to visual experience but are part of a general computational system.

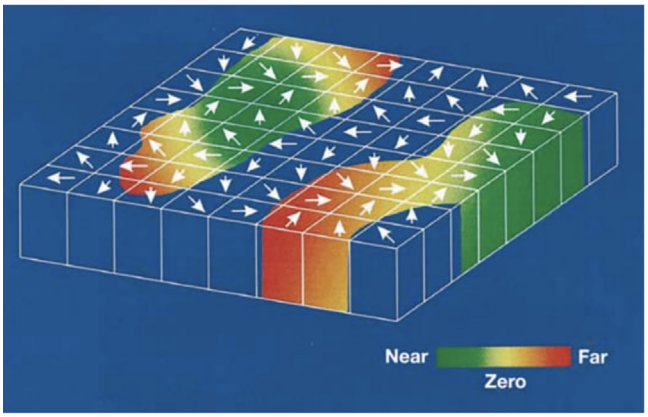

Fig. 11 A schematic representation of macaque V5/MT as a slab, subdivided into columns. Arrows represent the motion direction that most strongly activates neurons in a column, which forms a feature-based map. Preferred binocular disparity is superimposed on this map, ranging from strong (rainbows) and to weak (blue) tuning. From DeAngelis and Newsome (1999).

Perceptual experience

In certain parts of the visual system, the information defining a perceptual experience is spread across multiple interleaved mosaics. A classic example is color: three interleaved cone mosaics encode the retinal image. The response from only one of the mosaics tells us little about the expected color appearance. Consider that a bright blue sky excites the L-cones far more than candlelight; yet the candlelight appears more red. Color is clearly determined by a multidimensional initial encoding (Maxwell, 1860), and we might expect the same for other perceptual features.

A different view was proposed in a classic paper—in frog—which identified stimuli that were highly effective at exciting retinal cells. These stimuli were labeled "trigger features" (Lettvin et al., 1959), and the possibility was raised that signals by these cells indicated the presence of these features. Barlow suggested that at some point in the primate visual pathways the response of a single neuron might have a specific perceptual meaning: "High impulse frequency in such neurons corresponds to high certainty that the trigger feature is present (Barlow, 1972)." He proposed this as a "neuron doctrine for perceptual psychology."

There are three parts to Barlow's hypothesis. The first is that a strong response by a single cell can have a specific meaning. The second is that such cells are present at a "high-level" of the visual pathways, after preliminary processing. The third is that at this high level the neural activity must be sparse. If every cell has a specific meaning—its trigger feature—sparsity is a logical necessity. Otherwise, we would experience many conflicting percepts.

Sparsity

Sparse responses are important for another reason: The brain consumes a great deal of energy, and sparse responses are energy efficient responses. According to one estimate, "The cost of a single spike is high, and this severely limits, possibly to fewer than 1%, the number of neurons that can be substantially active concurrently" (Lennie, 2003).

Spareness may be common across much of the cortex, but the prediction of increasing spareness along the visual hierarchy does not match experimental data. For example, the sparsity of action potentials does not increase sharply when comparing a relatively posterior map (V4) and anterior region (IT). Rather, the main difference is that in the anterior map, the neuronal responses become more selective for object categories (say, faces) and also more tolerant to variations in the stimulus itself (say, size or position) (Rust and DiCarlo, 2012). This tradeoff maintains a constant level of sparseness between the visual brain areas.

The sparsity principle has led to interesting experiments in building artificial systems. When trained to encode natural images subject to a sparsity constraint, these systems develop encoding neurons with receptive fields that match the properties of V1 neurons (Olshausen and Field, 1996a,b). Sparsity has also been very useful in developing ideas about compressive sampling (also called compressive sensing). This is the discovery that the number of samples needed to reconstruct a signal without error can be smaller than expected by the Nyquist/Shannon sampling theorem (Candes, 2006). Compressive sampling also has application to information representations in neuroscience (Ganguli and Sompolinsky, 2012).

Asynchronous systems

Almost nothing about visual system circuitry is synchronous. The absence of a master timing circuit is evident from the fact that (a) photoreceptor latencies differ between types and across the retina (Baudin et al., 2019; Sinha et al., 2017), (b) signals from RGCs at different locations respond asynchronously to events within their receptive field, (c) cortical pathway latencies differ between circuits and stimuli (Albrecht et al., 2002; Nowak et al., 1995), and (d) for certain dynamic stimuli, perceptual judgments of color and motion are temporally mis-aligned (Cavanagh et al., 1984; Moutoussis and Zeki, 1997; Wandell et al., 1999).

Despite these multiple asynchronous systems and eye movements, we experience a stable scene. Some argue that stable perception of an asynchronous system must be instantiated in a single location in the brain (Zeki, 2015); others accept the idea that a percept is a distributed representation without a unique localization (Mcclelland et al., 1987).

A theory of a system with asynchronous components has certain requirements. We can understand some of these requirements by considering the design of modern cameras, which generally acquire a small collection of images and then recombine them into the image shown to the user (multi-capture, single image). These systems require at least short-term memory to store the multiple images at different times, and scratch space to perform intermediate computations (alignment, data combination, (Wandell et al., 2002). This suggests that we should be exploring visual system components that serve as short term visual memory, a concept that has long been part of the psychological literature (Ishai and Sagi, 1995; Luck, 2007).

The asynchronous character of biological vision inspired an engineering design of event-based cameras (Gallego et al., 2022). Event-based designs have potential advantages for dynamics, bandwidth, and energy consumption. However, there are few algorithms designed to use event-based data to identify scene properties such as objects, color, or motion. It is an interesting and open field in which engineering algorithms and neuroscience investigations might cooperate.

Bayesian inference

Helmholtz's suggestion was that a central principle of visual processing is that the nervous system creates a perception of "such objects … as would have to be there in order to produce the same impression on the nervous mechanism." Today, we refer to

this as solving an inverse rendering problem. The camera—or eye—measures the scene radiance and estimates the objects and lighting that would produce the encoded signal (Spielberg et al., 2023).

The information the retina encodes is insufficient to guarantee a unique solution, so we say the inverse problem is ill-posed (i.e., there are many possible solutions). Bayesian inference is the idea that we should choose the most probable solution (Ma et al., 2023). In many cases we do not have enough information to compute these probabilities. Even so, we must create some estimate, and this determines the selection (Wandell and Brainard, 2021).

There are a wide range of tasks where Bayesian inference can be applied, ranging from summarizing the relationship between neural subpopulations (Douglas and Martin, 2004), estimating a scene property (Brainard and Freeman, 1997), or framing hypotheses about the current situation, things, and environment (Barlow, 2001; Braitenberg, 1978). This is what Marr likely meant when he wrote that goals are part of the computational theory (Marr, 2010).

An important new approach to solving inverse problems is neural network technology (deep learning). These algorithms use data to build models that predict system responses and, when successful, generalize accurately beyond the scope of the measurements. There are a number of ways that networks can be trained, including supervised learning in which the network is trained on labeled data, unsupervised learning, reinforcement learning, and self-supervised learning (Goodfellow et al., 2016). Learning from the data can be formulated in such a way to turn the network into a Bayesian inference system, where the statistics are in the training data (Jospin et al., 2022).

Neural networks for modeling the visual pathways are at an early stage of development. Most do not incorporate many of the experimental measures of the visual pathways with any detail. For example, they are built on simple mechanisms without the diversity of neural signaling mechanisms. They do not incorporate the fovea and eye movements, asynchronous processing, or parallel channels. They are evaluated by how well the neurons in a trained network match generic pyramidal cells, but not the full range of circuitry (Yamins et al., 2014; Zhuang et al., 2021). Work towards implementing more realistic models, such as incorporating retinotopic constraints, is emerging (Finzi et al., 2023), and the night is young.

Conclusion

The complexity of the visual system, coupled with the current tools to measure the brain, motivate investigators to focus their analyses on system components. For this reason, most computational principles were developed to analyze or interpret data from one of these components in isolation. Receptive field models of V1 neurons, for example, do not typically make use of specific knowledge of the eye's optics despite the clear dependency. There is great value in building models that account for the impact of the different components, particularly if there is an interest in diagnosing which parts are failing. Some progress on visual algorithms can be made without specifying the contributions of different biological components, which is called a phenomenological approach.

A computational model of a complex system, whether a physical asset or a biological system, is called a digital twin. The value of such models to validate and diagnose the performance of engineering devices is increasingly recognized (Benson, 2023). There is much interest in creating digital twins for biology and health, even at the level of individuals for clinical diagnosis and monitoring. There are different approaches to building digital twins, reflecting different degrees of biological realism. At one end of the spectrum, the Human Brain Project aimed for a very realistic, but small scale, model (Wikipedia Contributors, 2024). At the other end of the spectrum are neural networks, which are relatively high-level phenomenological models of a broader scope of visual processing. This review provides some guidance about what is required to achieve different levels of biological realism.

A decade ago, the authors highlighted the vast amount of data available in visual neuroscience, and we noted the gap between this data and a unified theoretical understanding of the brain (Wandell and Winawer, 2011, p. 732). This gap remains, but the opportunities have shifted dramatically. New computer hardware has fueled an explosion in data collection, allowing researchers to create digital twins of the brain and build neural networks of unprecedented scale. These technologies were unimaginable a decade ago. We believe these new computational tools offer hope for deeper theoretical understanding and an opportunity to implement digital twins with different degrees of realism. The search for principles and computational models have the potential to help us integrate the vast array of data into a more comprehensive understanding of the visual brain.

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