

Review Article

Visual representation and perception

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Serial hierarchical processing, parallel processing and remapping on a dynamic network of several cortical visual areas are accountable for visual perception. Perception is organized in craniometric coordinates based on retinotopic maps of the layers of the lateral geniculate nucleus that project to the visuotopic map in the primary visual cortex. After perceptual completion and filling in the neural representation, it becomes a binocular visuotopic representation. Perceptual completion hosts integration, which implies the reconstruction of the form perception of partial contour information. The V1 visuotopic map creates a stereoscopic map based on the disparity of the monocular information. This stereoscopic map is distinct from each of the monocular maps, although there is one eye that is always dominant for the location of a target. Craniocentric neural representation of the visual scene is perceptually stable, regardless of eye movements. Keeping the head in one position and scanning the scene with the eyes, we reconstructed a high-resolution scenario. Remapping and efferent copies of the eye movements made this scene stable and entirely in color. By moving the head, we generated different craniocentric maps, which are perceptually stable regardless of the eye movements. The ambient map is a conscious reconstruction of the scene with optimizations of resolution, color, and contrast across the entire field of view. For each position of the head, the oculomotor system scans the scene with the eyes using foveal vision to construct a high-resolution color scenario that generates an optimized visual representation. A large scenario is reconstructed piece by piece on a dynamic topographically organized network made up of virtually all cortical visual areas.

Key words: Visual system, visual topography, visual representations, remapping

INTRODUCTION

Vision is the ability to understand the surrounding ambient environment using light reflected from the objects. The resulting perception is otherwise known as eyesight or visual perception. Vision is a universal experience used for reading, hand and body coordination and to navigate or orient in the ambient environment. Reading comprehension is the ability to deal with text, understand its meaning, and integrate with what the reader already knows. Reading comprehension depends on visual acuity, and the ability of the interpretative faculty of the brain. There are several systems in the brain that participate in vision. The main and more important is the retina- geniculate- striate system responsible for visual acuity, depth and color perception, among others. The cortical target of this system is the striate cortex, also called the primary visual cortex or V1. The evidence that we have more than one system comes from anatomy and the ability known as blindsight. In this condition,

functionally blind individuals, who are cortically blind due to lesions in their striate cortex, respond to stimuli they are not consciously aware of. There is compelling evidence that blindsight occurs because visual information is conveyed through other routes bypassing the primary visual cortex (Covey, 2010).

LITERATURE REVIEW

In this review, we examine the different streams of visual information processing and the effect of perceptual completion and filling in on the retina- geniculate- striate system. We focus on visual representation in the brain and its effect on vision. We describe the visual representations as retinotopic, visuotopic, craniocentric or ambient maps. We propose that visual information be kept in a large and stable neural network composed of virtually all visual areas and connected with the various processing pathways. These pathways extract the information necessary to identify objects (ventral stream), to understand language (lateral stream), to compute the trajectory of a target and/or to understand social interactions (dorsolateral

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stream), and to allow motor coordination for body movement, such as stepping and locomotion (dorsomedial stream). This review is a shorter and updated version of the review previously published (Gattass et al., 2020).

Visual perception

Numerous studies in anatomy, neurophysiology and brain imaging have challenged the understanding of visual processing in the brain. Different works have shed light on the understanding of visual perception, each emphasizing distinctive attributes of vision. The early work of Daniel & Whitteridge (1961) emphasized the topographic organization of the primary visual cortex and its relation to visual acuity. They showed that the magnification factor of the central vision was significantly higher than that of the visual periphery and suggested that this organization would account for the difference in visual acuity. Parallel pathways of visual processing begin within the retina with different classes of ganglion cells projecting to different subcortical structures, which in turn project differentially to cortical areas. The ganglion cells project to different subdivisions of the dorsal lateral geniculate nucleus, which in turn project to different regions of layer IVc in V1. Separate compartments of V1 project to different CytOx-rich and CytOx-poor stripes in V2 or to MT (V5). We have been working with the notion that most visual processing is performed in cortical modules. Ascending circuits and intrinsic circuits build cortical modules to decode specific attributes of the sensory system. In the visual system, orientation modules were described first by Hubel and Wiesel (1968). They also proposed a hierarchical model for visual processing. This model implies that the concentric receptive field of the dLGN assembles orientation decoders or orientation selective cells arranged in columns to build in simple cells in V1, which would produce complex and hypercomplex cells. They imply that these columns would form edge detectors used in higher areas, such as the inferior temporal cortex, to assemble objects or form detectors, such as cells selective for faces (grandmother cells) described by Gross and collaborators (1972). Hierarchical theory is the foundation for serial processing in the visual system (Hubel et al., 1968). The discovery of several areas with topographically organized maps (Daniel et al., 1961 - Gattass et al., 1981), with modules selective for different attributes of the visual stimuli, such as motion or color (Zeki, 1974), creates the basis for parallel processing in the cortical visual areas. Frequency limitations of neural processing have suggested that parallel processing is accountable for the efficient detection of an image. Several areas work simultaneously, in parallel, to allow for fast processing of the visual scene. The very nature of the neural signals and the connections between visual areas, with action potentials with durations on average of more than 1 ms, limits the propagation of the visual information to less than 1 kHz. The interaction of cortical modules or synchronization between neurons is limited in a band of 1 to 300 Hz. Nonetheless, when we open our eyes, we build a stable perception in approximately 300 ms. Thus, parallel processing is a crucial mechanism to achieve this performance.

Processing of different attributes of the scene are necessary to accomplish parallel processing: V1 (orientation columns: orientation selectivity, main attribute for form perception,

perceptual completion, an attribute for the representation of an object), V2 (retinal disparity, attribute for 3D) (Pettigrew et al., 1968), V4 (color selectivity, attribute for color vision) (Zeki, 1974), MT (axis of movement columns, attribute for perception of motion) (Albright, 1984). In macaques, visual area V2 is the earliest site in the visual processing hierarchy in which neurons selective for relative disparity have been observed (Pettigrew et al., 1968, Thomas et al., 2002). By combining optical imaging, single unit electrophysiology and Cytochrome Oxidase (CO) histology, Ts'o and collaborators (2001) revealed in greater detail the functional organization within the CO stripes of the visual area V2 of primates.

Ungerleider and Mishkin (1982) proposed the concept of visual information processing streams. They defined a ventral and a dorsal stream, the first related to object recognition and the second related to motion processing. We propose that feed forward and feedback connections play an important role in determining the activity of each module in a wider network. For example, the activity of a locus in V1 may depend on the activity of several loci of extrastriate areas located anteriorly (Gattass et al., 1990).

With the description of visual area PO, it was suggested that the dorsal stream would be subdivided into a dorsal medial and a dorsal lateral stream (Gattass et al., 1990, Nascimento-Silva et al., 2003). The new dorsal medial stream is related to locomotion processing (Neuenschwander et al., 1994). The concept of visual information processing evolved in nonhuman primates toward three streams, with the primary relay area receiving direct projections from the striate cortex (Zeki, 1974, Colby et al., 1988). We extended this concept to four streams of information processing in humans, as illustrated in Figure 1. The different streams receive most of the connection from discrete portions of V1 (Figure 1). The ventral stream receives central projections to 30° of V1, the ventral lateral stream is related to reading and receives projections from the central 4–5°, the dorsal lateral stream receives projections from the central 60°, and the ventral medial stream receives projections from the peripheral field 8–90°.

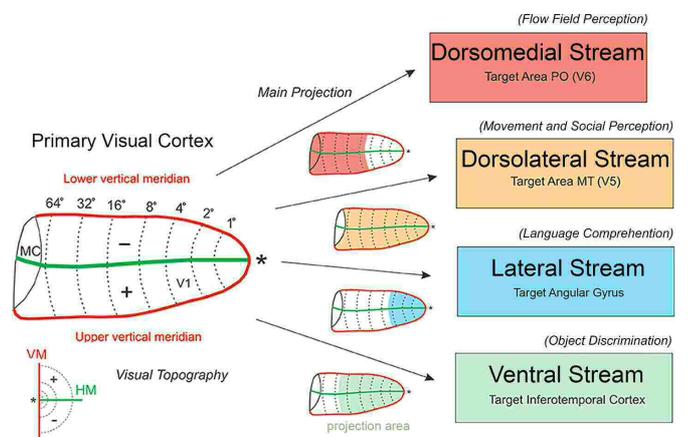


Figure 1. Visual streams of visual information processing. The flattened map of homo V1 with the vertical meridian is represented by black squares, the horizontal meridian by black circles, the eccentricity lines by dashed lines, and the visual field periphery by black triangles. Four cortical streams of visual information processing.

One example of selectivity at a global aspect, such as a monkey face, in the inferotemporal cortex was shown by Desimone and collaborators (1984) with the response of an IT neuron to monkey faces, a human face and a human hand. Scrambling the internal features of the face strongly inhibited the response, indicating that a particular configuration of the internal features was essential.

Streams of visual information processing

Figure 1 shows four streams of visual information processing related to different aspects of visual perception. The ventral pathway composed of projections representing the central visual field (about 20° of eccentricity) to inferior temporal areas is responsible for recognizing objects and faces; the lateral pathway composed of foveal projections (about 5° of eccentricity) to the angular gyrus and to Wernicke area, responsible for language comprehension; the dorsolateral pathway composed of binocular field projections (about 60° of eccentricity) to areas of the superior temporal sulcus, responsible for the perception of movement, processing of target trajectories and social interactions; and the dorsomedial pathway, consisting of projections representing the peripheral visual field to areas of the parietooccipital sulcus and the parietal areas responsible for motor coordination underlying walking and body movements. This figure emphasizes the extent of the visual field of V1 projecting to these streams. Most, if not all, streams receive direct projection from V1 to its initial target area. The direct projection from V1 to Wernicke's area or the angular gyrus in humans is still an issue. We have no direct evidence in humans of the projection of V1 to this area; however, the temporal association cortex is considered a primate specialization and is involved in complex behaviors, with some particular characteristics of humans, such as language. The emergence of these behaviors has been linked to major differences in temporal lobe white matter across several anthropoid primates (Roumazeilles et al., 2020). These differences parallel the differences in the white matter bundles leaving the occipital pole, the posterior arcuate fasciculus and the vertical occipital fasciculus (Weiner et al., 2017).

The study of nonhuman primates confirmed a direct projection from V1 to V2, MT and PO (Cragg et al., 1969 -Kuyper et al., 1965). The visual topography of V1 in humans is shown on the left in this figure and points to a geometric decay of the magnification factor with the isoeccentricity lines equally distributed at 1, 2, 4, 8, 16, 32 and 64 degrees. Most of the available data from functional MRI focus on the ventral stream of information processing as described by Ungerleider and Mishkin (1982). It is comprised of V1, V2, V3, V4 and TEO projecting to several areas in the temporal lobe. In this stream, there are descriptions of areas responsive to faces, hands and houses located in the temporal lobe (Kanwisher et al., 1997 - Pitcher et al., 2019). The fusiform face area in the temporal lobe is specialized for expert object recognition (Gauthier et al., 2000). We probably spend more time looking at faces than at any other object. We, therefore, associate this stream with object discrimination.

When humans read written words while they are in an MRI machine, they activate the opercular and central representation of V1 in addition to areas in the left occipital gyrus, while

listening to a word activates the auditory areas and areas in the temporal lobe known as the Wernicke area in the superior temporal gyrus (Baars et al., 2010). High span readers showed more activation in the left angular gyrus (Buchweitz et al., 2009). These results corroborate previous studies of listening and reading comprehension (Constable et al., 2004 - Michael et al., 2001). Activation of the central striate cortex was also observed by Bavelier. This stream we named here the lateral stream. It could be considered as the cognitive stream. This stream is used for reading, and most of the acuity tests used in ophthalmological practice probe its properties. Patients with macular degeneration lose the very central region used for reading. The foveal region in primates extends by approximately 5 degrees. The largest letter generally used in the acuity test (letter E) encompasses approximately 20 minutes of arc. Thus, in general, the tests used in clinical ophthalmology test this stream and not the dorsolateral stream that underlies visuomotor coordination. Behavioral data from patients with macular degeneration disease point to the existence of a new stream of visual information processing dealing with language. Patients with advanced macular degeneration are unable to read with their peripheral vision.

Eichert et al. investigated the extent to which between-species alignment, based on cortical myelin, could predict changes in connectivity patterns across macaques, chimpanzees, and humans. They knew that evolutionary adaptations of the temporoparietal cortex are considered to be a critical specialization of the human brain. They specifically addressed how language evolved in primates. Eichert et al. (2020) showed that this difference cannot be explained solely by changes in the positions of brain regions. Instead, the arcuate fasciculus underwent additional changes in its course, which may have contributed to the evolution of language.

Most of the visual field representation, including the binocular representation of the visual field, projects to the dorsolateral stream of visual information processing, which includes areas MT and MST (Tootell et al., 1995) and areas in the intraparietal sulcus and parietal areas. These areas interact with sensory-motor areas and are responsible for the perception of the movement of objects and visuomotor coordination (Gattass et al., 2020). This stream is used to aid most body movement and, in the ability to drive a motor vehicle. We consider the use of acuity tests to renew a driver license to be inappropriate. Visuomotor tests in the binocular region are indeed more appropriate. Recently, Picher and Ungerleider (2021) proposed a third pathway projecting from the early visual cortex, via motion-selective areas, into the Superior Temporal Sulcus (STS). Studies demonstrating that the STS computes the actions of moving faces and bodies (e.g., expressions, eye gaze, audio-visual integration, intention, and mood) show that the third visual pathway is specialized for the dynamic aspects of social perception (dorsolateral pathway in Figure 1).

In the dorsomedial stream, the peripheral field of V1 projects to areas PO and POd, areas in the intraparietal cortex and areas in the parietal lobe. These areas are organized in the isopolar domain and are probably suited to process centrifugal and centripetal movement of objects. These areas project to areas of the intraparietal sulcus and to areas of the parietal lobe (Colby et al., 1988, Ungerleider et al., 2008).

The visual representation at the conscious level as previously reported (Vernet et al., 2020) can be related to visual maps in the cortex. Intraub (2012) and Shioiri et al. (2018) proposed a new multistage model for visual scene representation in terms of an egocentric spatial framework that is ‘filled-in’ by visual sensory input, amodal perception, expectations and constraints derived from rapid-scene classification and object-to-context associations.

Perceptual completion and filling in

Perceptual completion is a phenomenon in which the contour and shape are perceived even though these features are not physically present in the retina. In the human retina, there is a region naturally devoid of photoreceptors called the blind spot. It corresponds to the head of the optic nerve. This discontinuity in the receptive surface, under normal circumstances, is not accompanied by abnormal perception, even in monocular conditions. Fiorani and his collaborators (1992) have shown that neurons within the cortical representation of the optic disk in V1 interpolate the receptive field position for the contralateral eye based on the extension of the stimuli beyond the boundaries of the blind spot (Azzi et al., 2015). In addition, they showed that the ability to interpolate receptive field position across substantial distances is present in neurons in additional portions of V1 (Botelho et al., 2014).

De Weerd and collaborators (1995) studied neural activity in different visual areas in awake behaving monkeys while fixating on a dynamic background. Using a patch located in the receptive field, we found that cells in visual area V3 after 6–8 s presented activity compatible with filling-in. Filling-in is a perceptual phenomenon in which visual features such as color, brightness, texture or motion are perceived in a region of the visual field, although such an attribute exists only in the surroundings. The time course of these dynamic changes in activity parallels the time course of perceived filling in of the hole by human observers, suggesting that this process mediates perceptual filling in (De Weerd et al., 1995, Gattass et al., 1999).

DISCUSSION

Visual representations in the brain

Figure 2 compares retinotopic (1) versus visuotopic representation (2). Different head positions generate distinct craniotopic maps (3 and 4). Regardless of head and body position the ambient map (5) prevails. A retinotopic map refers to the orderly mapping of the receptive field position in retinotopic coordinates in the brain. A retinotopic map implies the existence of a neuronal representation organized in retinotopic coordinates. Evidence for the existence of retinotopic maps and, by implication, localization of the function in the visual cortex came from analyses of visual field scotomas resulting from partial injuries to the visual cortex caused by bullet wounds sustained by soldiers in different wars. These studies showed a predictable relationship between the region of damage in the striated cortex and the location of the area of blindness in the visual field (Baars et al., 2010).

The map of V1 is visuotopic; that is, the area reconstructs the image representation based on predictable cues. If you view a newspaper page printed with many imperfections, we

automatically reconstruct the text or the imperfection (partially interrupted letter fonts) based on local circuits or feedback connections to V1. Thus, the representation of the image in the primary visual cortex is visuotopic and not retinotopic (Figure 2).

The visual perception is three-dimensional. It presents a number of properties described as perceptual completion in V1, filling in V3, stereoscopic responses (due to retinal disparity) in V2, and color representation due to the processing in V4. Visual representations in the neocortex are based on extensive parallel, serial and feedback circuit connections. It is stabilized due to feedback of the efferent copy of the control of the extracocular muscles. Remapping and perceptual inhibition are characteristics of image representation in the neocortex. If we keep our head in the same position, the representation of the image in the neocortex is stable, despite occasional eye movements. However, if one moves the head or the position of the skull in the ambient environment, the neural representation of the scene changes, and a new perspective of the image replaces the original perspective (Figure 2). There is no evidence for efferent copies of the medulla that command the neck muscles to the neocortex, and in this case, we have a craniocentric perception of the scene. The neuronal representation of the scene is also modified when we move forward or backward in the ambient environment. Centrifugal and centripetal movement of objects in an ambient environment generates maps used for visual motor coordination. These visual representations of the ambient environment are based on an egocentric map.

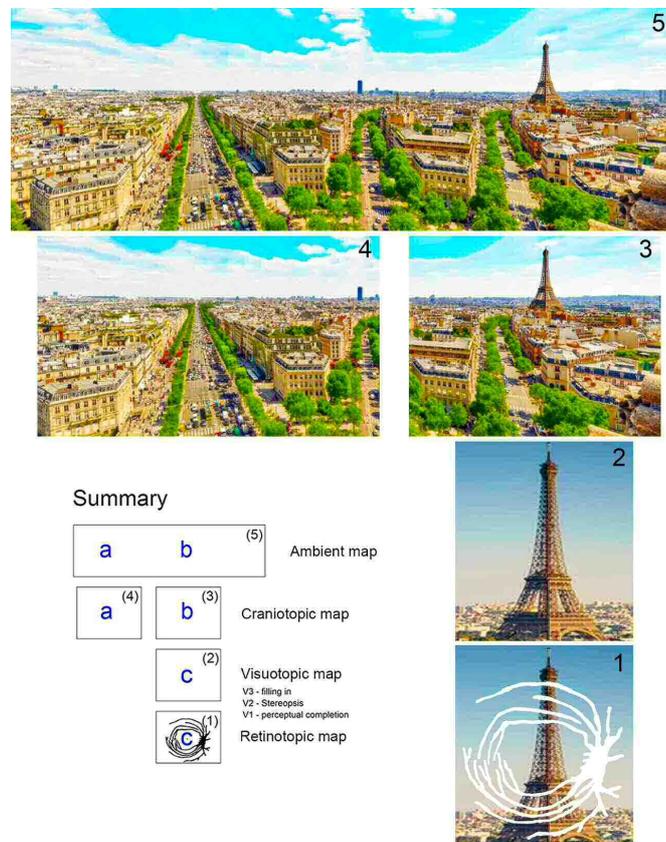


Figure 2. Neuronal representations. Representation of a retinotopic map of the Eiffel Tower (1) and a corresponding visuotopic map (2). Different craniotopic maps are shown in (3) and (4), depending on the position of the head. An ambient map (5) is an aerial view of Paris, France, assembled on a dynamic network in the cortex.:

Eye movement and remapping

When we move our eyes but maintained our head fixed, our visual perception is stable (Figure 3A-3D). Figure 3 compares the representations of the craniocentric map (Figure 3A) with V1 visuotopic maps (Figure 3B-3D). Additionally, we show the impact of an extrinsically induced eye movement on the visual perception (Figure 3E-3F). When we look at the waterfall based on the three fixation points (colored plus signs) the craniocentric perception is stable (Figure 3A) regardless of the changes in the retinal image and the corresponding V1 representations (Figure 3B-3D). Notably, the representation in the network of visual areas remains stable. However, if we move our head, the perception changes, and a new perspective of the visual scene emerges. This difference is related to the nature of the integration of the areas controlling eye movements and the areas controlling head movements and the cortical visual areas (Duhamel et al., 1992, Goldberg et al., 2002). Motor nuclei from extrinsic eye muscles are integrated into areas of the intraparietal cortex, while areas of the medulla controlling the neck muscles do not reach the neocortex. Spindles or movement receptors are well integrated into the cerebellum and are responsible for harmonious integration of the muscles, resulting in precise control of the movement of the head. Thus, stabilization by feedback of efferent copy of the eye movement generates a stable representation of the visual scene (Figure 3E), while the perception of the same scene during an extrinsic movement of the eye by tapping externally one eyeball with your finger causes a destabilized (fuzzy) perception (Figure 3F).



Figure 3. Perceptual spatial constancy in the presence of eye movements and visual perception with natural and artificial eye movement. The scene shown in A can be scanned with eye movements, but the perception of the image remains constant despite the different images represented in the retina (+ in B, C, and D). Image stabilization by feedback of the efferent copy of the eye movement (E) compared with the perception of the same scene while tapping externally one eye with your finger (F).

CONCLUSION

Vision captures information via discrete eye fixations, interrupted by saccadic suppression, and is limited by retinal inhomogeneity. However, scenes are perceived as coherent, continuous, and meaningful despite eye movements. In this review, we show the difference between retinotopic, visuotopic, craniocentric (or cyclopic) and ambient maps. The retinotopic map exist in subcortical structures, while the others are present in the neocortex. The ambient or egocentric map enables the relationship between the visual map and the motor map of the individual. It is important to translate the location of the skull-centered map to a location on the map of nearby extracorporeal space. It is also important to correlate visual space in nearby extracorporeal space during ambulation, as in the case of ambulation in an immersive bubble. The 3D map is a craniocentric, skull centric or cyclopic map. It is perceptually stable regardless of eye movements. Keeping the head in one position and scanning the scene with the eyes can reconstruct a scenario with high resolution by scanning the scene through the eyes, using the foveal region of the retina to build the scene. This scenario held in a large dynamic network is stable, with high resolution, entirely in color, regardless of eye movements. High acuity is dependent upon the density of ganglion cells in the retina and its projection to the primary visual cortex, V1. This representation is reconstructed in the neocortex in a set of areas that constitute a very efficient network to generate a percept with high resolution that spreads out toward the visual mid-periphery up to approximately 40°. We propose that both the high resolution and the color information propagate in the network toward the representation of the periphery. Our conscious perception of the scene for each position of the head is stable and uniform. The ambient or egocentric map is a conscious 3D reconstruction of the scene with optimizations of resolution, color, and contrast across the entire field of view. It is built from several contiguous craniocentric representations. For each position of the head, the oculomotor system scans the scene using the eyes, specifically its foveal regions to construct a high-resolution color scenario that is updated based on an expected visual model generated by the network.

Thus, a large scenario is “constructed” piece by piece in the network to allow for the reconstruction of the ambient scene. It is useful to compute object trajectories in space, to estimate the location of static and moving objects, and to estimate distances to compute direction and changes in trajectories. This representation is crucial to navigate in 3D space, to determine road trajectories and to estimate spatial relations across landmarks.

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CONFLICT OF INTEREST

None declared

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