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VISION: A SYSTEMS NEUROSCIENCE PERSPECTIVE GÖRME: SİSTEMSEL SİNİRBİLİMİ BAKIŞ AÇISI

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Abstract

The visual system is the most studied part of the cortex, providing a basis for understanding not only visual processing per se but also the fundamental operations of the brain in general. Significant progress has been made in understanding neural structures sensitive to different visual attributes such as form, surface brightness, color and motion. Here, the basic neural structures and processing pathways for these visual features are reviewed. Dysfunctions in these processing pathways lead to deficits in the perception of different aspects of a visual object. In recent years, there is a growing interest in applying accumulated knowledge in vision science to investigate altered neural structures and abnormal perceptual processing observed in neurological disorders. Key issues and clinical studies are also discussed within the context of visual feature processing.

Keywords: visual cortex, dorsal pathway, ventral pathway, form perception, surface brightness, color, visual motion, abnormal visual processing

Özet

Görsel sistem korteksin en çok incelenen parçasıdır. Bu durum görsel sistemin sadece görmenin temelindeki sinirsel işlemler hakkında değil beynin genel çalışma prensiblerini anlamaya dayalı bir temel teşkil etmesinden kaynaklanmaktadır. Şu ana kadar farklı görsel özelliklere (örneğin şekil, yüzey aydınlığı, renk, hareket) duyarlı sinirsel yapıları anlamaya yönelik çok önemli ilerleme kaydedilmiştir. Bu makalede, görsel özelliklere duyarlı temel sinirsel yapılar and işlevsel yollar gözden geçirilmiştir. Herhangi bir işlevsel yoldaki fonksiyonel bozukluk farklı görsel özelliklerin algısında eksikliklere yol açmaktadır. Son yıllarda, görsel bilimdeki bilgi birikimini nörolojik bozukluklarda rastlanan sinirsel yapı değişikliği ve buna dayalı anormal algısal işlemleri anlamada kullanmaya yönelik artan bir ilgi bulunmaktadır. Bu yönde gerçekleştirilmiş kilit konular ve klinik çalışmalar da görsel özellik işleme bağlamında tartışılmaktadır.

Anahtar Kelimeler: görsel korteks, dorsal işlevsel yolu, ventral işlevsel yolu, şekil algısı, yüzey aydınlığı, renk, görsel hareket, anormal görsel işleme

1. Introduction

A central problem in systems neuroscience is to understand how neural activity gives rise to perception and behavior. Vision provides an excellent model system to study how this happens. One third of the human cerebral cortex is dedicated to analyzing visual information and the processing hierarchy for visual information is very similar to the general functional structure in the brain. Therefore, deep understanding of visual system provides substantial information in order to shed light on this central problem of systems neuroscience. As a consequence of its general importance, the visual system is the most thoroughly studied of all sensory systems. The general organization, key neural structures and processing pathways have been identified for different aspects of a visual object such as form, surface brightness, color and motion.

I begin this review article with the overall organization of the visual system and key neural structures for vision. Developments in systems neuroscience and computational modeling suggest the existence of separate pathways for processing different attributes of a visual object. These developments and the data that support the existence of distinct processing pathways is the primary focus of the

review. Moreover, dysfunctions in these distinct visual pathways and their influences on perception are discussed within the context of recent studies on schizophrenia.

2. Organization of the visual cortex

The visual system consists of hierarchically organized distinct anatomical areas (Felleman & Van Essen, 1991). These visual areas are interconnected through ascending feedforward projections, descending feedback projections, and projections from areas at the same hierarchical level (Van Essen & Gallant, 1994). The visual areas and their connections with each other lead to distinct pathways functionally specialized for processing different aspects of a visual object (Figure 1a). In fact, this specialization starts from the retina. There are three types of retinal ganglion cells magnocellular, parvocellular and koniocellular (Merigan & Maunsell, 1993). Magnocellular and parvocellular cells constitute the major population of the ganglion cells (90%). Magnocellular cells have fast-phasic responses, larger receptive fields and a rapidly saturating contrast response, whereas parvocellular cells have slow-tonic responses, smaller receptive fields and a linear contrast response (Kaplan & Shapley, 1986;

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Purpura et al., 1988; Schmolesky et al., 1998). These two populations of cells project to distinct layers of the lateral geniculate nucleus (LGN) and form two afferent pathways, the magnocellular (M) and the parvocellular (P). In addition to these feedforward connections, the LGN gets most of its input from the higher visual areas by feedback connections and acts as a regulator or filter of information passing to the cortex (Lamme & Roelfsema, 2000; Merigan & Maunsell, 1993).

The parallel pathways (M and P) start intermixing in the cortex (Merigan & Maunsell, 1993; Van Essen et al., 1992). In the primary visual cortex (V1), located posteriorly in the brain, neurons code simple features of a visual stimulus, such as orientation and edges. Moreover, neighboring points in the retinal image are projected onto neighboring points in cortex. This type of mapping is referred to as retinotopy. Further functional subdivisions and arrangements of neurons in V1 (blob and interblob regions) and V2 (thick, thin, and interstripe regions) have been identified by using a technique called Cytochrome Oxidase (CO) staining (Horton, 1984; Horton & Hubel, 1981; Tootell et al., 1983). The blobs in V1 contain neurons that are selective for color and relatively unselective for orientation. However, the opposite is true for the interblob regions (Livingstone & Hubel, 1988). Corresponding properties are found in the thin stripes and interstripes in V2 and color-sensitive neurons are far less common in V1 layer 4B (Lamme & Roelfsema, 2000).

In higher visual areas, more anterior in the brain, increasingly more complex features are processed. Receptive fields become larger and retinotopy breaks down. According to their connections, two cortical pathways emerge: dorsal and ventral (Figure 1a). The dorsal, magno-dominated, pathway flows to MT(V5) and parietal cortex and is mostly involved in space, movement and action. The ventral, parvo-dominated, pathway flows into temporal areas and is mostly concerned with object and pattern recognition (Milner & Goodale, 1995; Mishkin et al., 1983). Furthermore, large differences exist between response latencies of dorsal and ventral stream areas partly because of the different temporal dynamics of the magno- and parvo- pathways feeding into these areas.¹

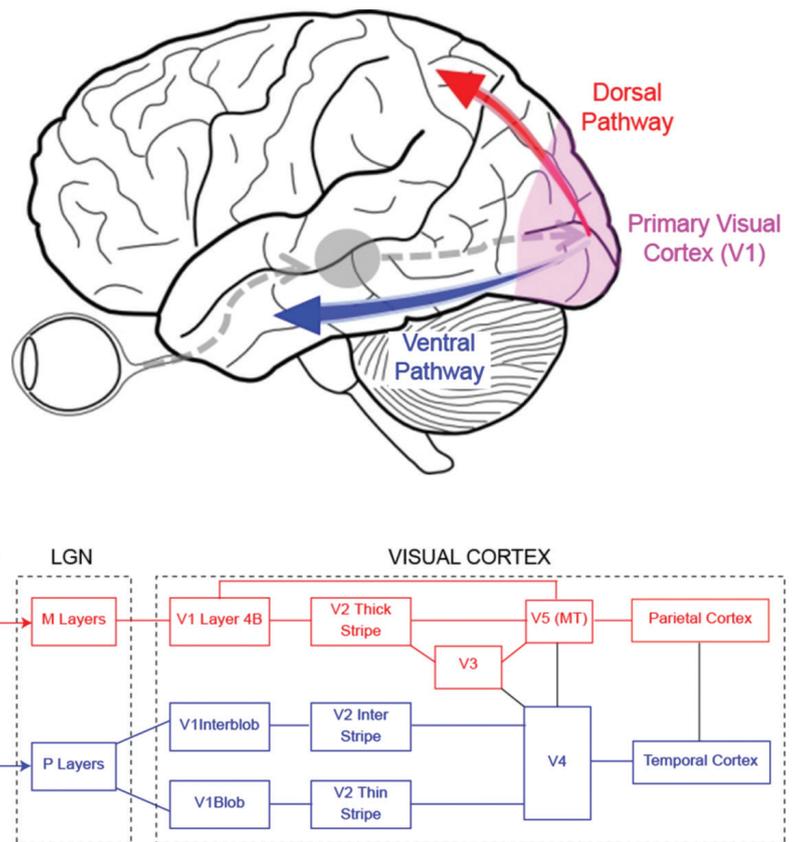


Figure 1. Hierarchical organization of the visual system. a) Schematic illustrating information flow from retina to primary visual cortex (V1) through lateral geniculate nucleus (LGN). The gray circle corresponds to LGN and the dashed gray arrows represent anatomical connections from retina to visual cortex. After primary visual cortex, visual processing continues in dorsal (red) and ventral (blue) pathways. b) The segregations and connections between early visual areas. Boxes correspond to visual areas or neural structures/ compartments within a visual area. The connections between different neural structures are represented by solid lines. To avoid clutter, only key neural structures and connections are shown.

3. Processing pathways for different attributes of a visual object

Form, Surface Brightness and Color

Perception of form (i.e., contour) and surface features (e.g., brightness and color) are essential for recognition of objects in the environment. It is widely believed that these features are processed by different sub-systems within the parvo-dominated ventral pathway. Neurons at early stages of the visual system (V1 interblob) have orientation selective receptive fields and these receptive field types are accepted to contribute to the functional basis of form perception (Hubel & Wiesel, 1962). The outputs of these oriented contrast detectors are grouped over spatially long distances to generate the outline of a visual shape at the later stages of the processing stream. Form processing continues mainly by neurons in V2 interstripe and neural compartments in V4 specialized for shape processing. On the other hand, brightness and color processing is mostly carried out by neurons in V1

¹The interactions between two pathways at different hierarchical levels are essential. Early level interactions and their perceptual consequences are briefly mentioned within the context of backward masking in the following sections.

blob, V2 thin stripe and neural compartments specialized for surface features in V4 (Figure 1b). Accumulating evidence by experimental and modeling studies support the existence of two sub-systems and also report that their processing dynamics is different: a fast system concerned with extracting contours and a slower system with assigning surface brightness and color (Breitmeyer et al., 2006; Grossberg & Mingolla, 1985; Lamme et al., 1999; Rogers-Ramachandran & Ramachandran, 1998).

In order to have a coherent representation of a visual object, these two sub-systems processing complementary information must be able to communicate and interact with each other. Several perceptual completion phenomena suggest that the interaction is achieved by means of spreading mechanisms and filling-in. The filling-in hypothesis states that brightness is perceived via a filling-in process initiated by luminance contrast boundaries. In some way, a response initially biased toward the boundaries fills-in to represent the interiors of uniform surfaces (Neumann, 2003; Pessoa et al., 1998). The filling-in hypothesis is supported by many studies (Pessoa et al., 1998). An interesting behavioral demonstration is designed by Paradiso and Nakayama (1991). They used a visual masking paradigm to investigate the role of edge information in determining the perceived brightness and the temporal dynamics of proposed filling-in hypothesis. In their experiments, they used a disk as a target. The disk was briefly flashed and after a variable stimulus onset asynchrony (SOA), a mask was presented. In different stimulus configurations, the mask stimuli consisted of a bright line, a circle, or an incomplete rectangle. For SOA values between 50 and 100 ms, the brightness of the central area of the disk was greatly reduced. The brightness of the central region was largely unaffected for SOA values greater than 100 ms. The striking result is that the decrease in perceived depended on the distance between target and mask and maximal suppression occurred at later times for larger distances. Basically, the temporally following contour mask seems to suppress the active spreading of the surface information in this visual phenomenon. Paradiso and Nakayama (1991)'s results are consistent with the hypothesis that brightness signals are generated at the borders of their target stimuli and propagate inward at a rate 6.7-9.2 ms/deg.

Visual motion

The processing of visual motion is essential for survival in a dynamic world. Visual motion is a source of information that can serve many functions for a behaving animal. These functions include establishing the three dimensional environment, estimating other objects' trajectories and velocities (Nakayama, 1985). One of the earliest computational models of motion detection was developed by Hassenstein and Reichardt (1956). Their behavioral measurements from *Cholorphanus* beetle led to a correlation model which is known as the "Reichardt detector". In order to detect motion, a Reichardt detector requires three basic operations: sampling, asymmetry, and nonlinear interaction. The input should be sampled at more than one location since motion is a vector that needs at least two points for its detection. These sampled data have to be processed in a slightly different way from each other to discriminate the direction of motion.

Otherwise, the inputs to the Reichardt detector could be interchanged without affecting the output. Thus, the detector would not be directionally selective if it were symmetric. Furthermore, the outcomes are combined and compared by using a nonlinear operation. A simple way to do this final step is by multiplying (correlating) the two processed inputs. A similar motion detection mechanism was identified by neurophysiological studies of rabbit retina (Barlow & Lewick, 1965). Later, motion energy models were proposed as an alternative to the correlation models. Motion energy models emphasize the processing of motion in the spatiotemporal frequency domain. Although the underlying computations of the two models are equivalent, their neural implementations are different and later neurophysiological experiments from visual cortex appear to support the motion energy model implementation (Albright & Stoner, 1995; Borst, 2000; Clifford & Ibbotson, 2003).

These early models of motion detection assume that our perception of motion is driven by first-order changes in the intensity of light on the retina. However, subsequent psychophysical experiments have shown that we can still perceive motion in the absence of first-order cues, when only second-order properties of the image such as contrast, chromatic content or spatial frequency change. Motion systems which are sensitive to the first and second order properties of a stimulus are called first and second order motion systems, respectively. These two motion systems are primarily monocular. Moreover, third order motion systems are identified by several studies of motion perception (Lu & Sperling, 2001). Third order motion systems are binocular and extract motion information from the spatiotemporal properties of salience (figure ground). Higher level visual areas and processes such as attention mechanisms are involved in the third order motion systems (Lu & Sperling, 2001). As mentioned below, the distinction between different motion systems have also been identified by recent functional imaging studies (Claeys et al., 2003; Ho & Giaschi, 2009).

Although some of the cells in the retina and thalamus respond to moving contours, it is generally agreed that explicit computation of motion starts at the primary visual cortex (V1) by directionally selective cells (Blake et al., 2003; Hubel & Wiesel, 1962). The neurons in V1 have small receptive fields and can only detect local motion signals inside their receptive fields. So, directionally selective neurons in V1 are considered as the low level motion detectors and called "local motion detectors". This situation shows a certain limitation of this first stage motion processing and leads to a well-known aperture problem (Adelson & Movshon, 1982; Hildreth, 1984; Wallach, 1935). When an observer views a long straight line through an aperture, the observer cannot discriminate different motion directions of the long straight line and can only detect motion orthogonal to the local contour. The aperture problem implies that directionally sensitive neurons in V1 always respond to a contour that crosses their receptive field (Hildreth, 1984; Nakayama & Silverman, 1988). In order to overcome the aperture problem and to obtain a coherent pattern motion, the local motion signals need to be integrated. It is widely believed that this second stage of motion processing starts at middle temporal gyrus (MT) and neurophysiological

studies show that a substantial fraction of MT neurons have sensitivity to pattern motion (Rodman & Albright, 1989). Area MT gets most of its input from directionally selective cells in V1 and thick stripes of V2 (Movshon & Newsome, 1996; Zeki, 1974).² The integration of these local motion signals takes place in area MT and neurons in this area start responding to the true pattern motion with a 60 ms delay (Pack & Born, 2001).

Motion computation continues at the medial superior temporal area (MST). Neurons in MST have even larger receptive fields and show selectivity to binocular disparity and optic flow such as expansion and contraction. MST neurons are also sensitive to non-retinal information about eye movements (Blake et al., 2003; Duffy & Wurtz, 1991a, b). As one ascends the visual hierarchy in the magno-dominated dorsal pathway, cortical areas become sensitive to more complicated motion types. For instance, cortical area Inferior Parietal Sulcus (IPS: homologous to macaque area VIP and LIP) and lateral parietal cortex get input from visual and auditory areas and they can be selectively activated by both visual and auditory motion (Lewis et al., 2000). Inferior Parietal Lobe (IPL) gets activated by high-level attention based motion (i.e., third order motion) and it is considered a key neural structure for the bilateral higher-level saliency-based system (Claeys et al., 2003).

4. Dysfunctions in Visual Processing

Dysfunctions in early-stage visual processing impair our perceptual performance in a wide variety of visual tasks. These perceptual abnormalities have been documented even in neurological disorders (e.g., autism spectrum disorder, schizophrenia) and age related changes typically associated with higher-level cognitive processing (Butler & Javitt, 2005; Raudaia et al., 2010; Simmons et al., 2009). There has been an increasing interest to extend this line of research as an avenue to understand the altered neural circuitry and the resulting information processing for different aspects of a visual object in schizophrenia. Accordingly, several perceptual paradigms have recently been recommended for translational use in clinical trials by initiatives organized by National Institute of Mental Health (Gold et al., 2012; Green et al., 2009).

Several studies indicate that schizophrenic patients have abnormal form perception, contour integration as well as contextual influences on perceived brightness such as brightness induction and collinear facilitation (Green et al., 2009; Must et al., 2004; Yang et al., 2013). Even though these studies point out distinct early-stage dysfunctions in form and brightness processing, research using backward masking paradigm received the most attention. In backward masking, the visibility of a target stimulus is suppressed by a surrounding stimulus, called mask, following target. Typically, the reduction in target visibility is highest when the SOA between target and mask is around 30-80 ms. When the SOA becomes smaller or higher than this optimal value, the visibility of the target recovers. This U shaped nature of the target visibility has

been used as a tool to gain insights into the temporal dynamics of brightness perception and relative timing of signals ascending through the visual system via different pathways (Breitmeyer & Ogmen, 2006). The dual-channel hypothesis has been influential and leading approach to account for the neural mechanisms underlying backward masking (Breitmeyer & Ogmen, 2006). According to the dual-channel approach, a visual stimulus generates a fast transient and a slow sustained activity in M and P pathways, respectively. These two pathways start interacting at early parts of the visual cortex. The slow sustained activity of the target is inhibited by the fast transient activity of the following mask through interaction between these two pathways. This inter-channel inhibition depends on the SOA between two visual stimuli and it accounts well for the U shaped visual backward masking function. Several research groups independently found that schizophrenic patients show a larger magnitude of masking and the masking effect is prolonged to higher SOA values relative to healthy participants. These results have been interpreted by changes in the interaction between two pathways due to M pathway dysfunction in schizophrenic patients (Butler & Javitt, 2005; Green et al., 2011).

Another well documented atypical perception in schizophrenia is visual motion perception. Schizophrenic patients have lower sensitivity to global motion and poorer speed discrimination relative to healthy controls (Chen et al., 1999). Moreover, center-surround interactions such as motion repulsion have been found to be abnormal in schizophrenic patients (Yang et al., 2013). These studies together with findings from backward masking and neuroimaging emphasize early-stage dysfunctions in the magnocellular pathway and deficits in key neural structures in the magno-dominated dorsal stream. The relationship between the early stage dysfunctions (and resulting abnormal perception) and social aspects of schizophrenia is still not clear. Future studies aimed at understanding this relationship will have significant contributions to the development of diagnostic tools and strategies for the treatment of this mental disorder.

5. Concluding Remarks

The visual system is the most thoroughly studied of all the sensory systems. This is due not only to the importance of the area covered in the brain by the visual system but also to its organization and pathways for different attributes of an object such as form, color and motion. Information processing is distributed in that neurons specialized in processing different stimulus attributes such as color and motion tend to cluster in distinct anatomical areas. Moreover, these distributed activities at distinct anatomical sites have different temporal dynamics. Significant progress has been made in understanding how the spatio-temporally distributed processing dynamics of the visual system is correlated with the basic features of a visual object. The accumulated knowledge and paradigms developed in vision research can be applied for understanding early-stage dysfunctions

² Besides these early neural structures, several studies (e.g., Tootell et al., 1997) found that neurons in area V3A are sensitive to visual motion and they have strong direction selectivity.

in information processing and perceptual deficits in neurological disorders such as schizophrenia.

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