STRUCTURAL COMPONENTS INVOLVED IN THE HUMAN PSYCHOLOGICAL EXPERIENCE OF COLOR VISION

by

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ABSTRACT

The structural components and processes of the psychological experience of human color vision have been both admired and extensively studied throughout the course of human history. The purpose of this paper is to summarize this first-rate example of a psychological phenomenon that can be understood in physiological terms through literature review. At each level of processing, special attention will be given to the differing roles of magnocellular and parvocellular pathways starting with the early components of the visual system. Particular emphasis will be placed on magnocellular and parvocellular contribution at higher levels of processing, especially V1 and V2. The effort will be to progress though the more linear models of early processing to the more complex exponential models of later cortical perception in an effort to more thoroughly describe the holistic experience of color vision. In fact, we will find that as visual information proceeds through the various anatomical structures associated with vision, the distinct functions of magnocellular and parvocellular divisions, though still identifiable, become less exclusive.

Introduction

Louis Armstrong in his most recognized tune "What a Wonderful World" praises the wonders of the natural world with the words, "I see trees of green, and red roses too… skies of blue and clouds of white, the bright blessed day, and the dark sacred night." Clearly the capacity of the normal human visual system to experience the psychological phenomenon of color enriches visual experience and adds an element of beauty to the world around us. One may not consider the physiological processes involved in this ability particularly poetic, or feel a sudden inspiration to break into song about it. Even so, there remains a certain elegance in the neural anatomy responsible for color perception, and its necessity in this experience is certainly worthy of admiration.

The structural elements involved in vision have been studied extensively (Livingstone & Hubel, 1988). Color vision is just one component of that larger system and is supported by the same anatomical structures and neural pathways. Composed of anatomical structures in the eye, the lateral geniculate nucleus, areas of the visual cortex, and the temporal lobe, color vision is a first-rate example of psychological phenomenon that can be understood in physiological terms. In this linear model, one can broadly describe the transformation of light energy into a neurological signal, and consequently, a holistic visual experience. However, given the evidence pointing toward separate pathways throughout the visual system specialized for the analysis of different aspects of the visual image (i.e. form, color, movement, depth), a strictly linear model may not capture the complexity involved in color vision. The aim of this paper will be to present

evidence investigating the role of various structural components of the nervous system in creating the psychological experience we know as vision, and in particular, color vision. At each level of processing, special attention will be given to the differing roles of magnocellular and parvocellular pathways to this experience. Although early components of the visual system (i.e. cones, ganglion cells) will be discussed, particular emphasis will be placed on magnocellular and parvocellular contributions at higher levels of processing, especially V1 and V2.

The Early Visual System: The Retina

Functional differences in the various structures of the visual system begin early, even at the level of cones in the human retina. An image captured by the retina is composed of various spectral properties as a result of light being reflected of that object in physical space. The three types of cones in the retina, each containing a different version of the photopigment called retinal, respond preferentially to certain wavelengths of light (Livingstone & Hubel, 1988). The three cones are described as L cones, M cones, and S cones, named for their responses to light of long, medium and short wavelengths. When stimulated by their preferred wavelength, cones project action potentials to retinal ganglion cells, which are either larger magno-cells or smaller parvo-cells. These cells' axons then project from the retina to the lateral geniculate nucleus (LGN) via the optic nerve; the larger cells to the magnocellular layers of LGN (layers 1 and 2), and the smaller cells to the parvocellular layers of LGN (layers 3,4,5, and 6).

Receptive Fields

Centers of receptive fields in retinal ganglion cells vary, but cells are characterized by color-opponent mechanisms. For instance, some cells in the retina respond preferentially to long wavelength red light projected onto their receptive fields, as opposed to green light in the receptive field, and vice versa. Likewise, some cells are inhibited by short wavelength blue light and excitatory for yellow light and vice versa (Hering, 1964). Many of these cells are of the center-surround variety, characterized by different wavelength preferences in the center of the receptive field, than in the surrounding area. On-center cells are excitatory to a particular wavelength in the center of the cell, whereas off-center cells are excitatory in the area surrounding. Retinal ganglion cells gathering color information from the cones are classified as either larger magno-cells (M cells) or smaller parvo-cells (P cells).

P-cells seem to respond differentially to variances in wavelength messages coming from the cones (Wiesel & Hubel, 1966), leading to speculation that these P cells and the parvocellular pathway in general is specialized for color. On the other hand, M cells are typically understood to be orientation and motion sensitive, but recent studies have shown that M pathway activity can be suppressed in the presence of diffuse red background light as opposed to green or white light (Breitmeyer & Breier, 1994). Of particular interest at the perceptual level is the increased difficulty in discriminating the motion of objects at isoluminance (equal brightness of object and background), when they are in the presence of a diffuse red background (Breitmeyer & Williams, 1990; Breitmeyer

& Breier, 1994; Brown & Koch, 2000). This is most likely due to the red-dominant surround mechanism in the receptive fields of most M neurons (Wiesel & Hubel, 1966). Red light therefore activates, and in effect "ties up" the M pathway, making it more difficult to perceive motion of objects in the visual field.

Lateral Geniculate Nucleus (LGN)

The LGN is clearly divided into magnocellular and parvocellular layers. M cells in the retina project to the magnocellular layer, while P cells project to the parvocellular layer. P cells at the level of LGN continue the pattern of retinal ganglion P cells, which are tuned to two main color-opponent mechanisms. In a sample of 100 LGN cells, DeValois (2000) found these cells to be overwhelmingly tuned to the red-green and blue-yellow regions of the color axis. The authors conclude that processing of cone information up to and including the LGN is strikingly linear. They find that the responses of most LGN cells to chromatic information can be fit with a sine wave inclusive of the two main color-opponent regions along the color axis, contributed by input mainly from L cones and M cones, not from S cones.

Primary Visual Cortex (V1)

From the LGN, magnocellular and parvocellular regions project to various levels of primary visual cortex in the occipital lobe, commonly referred to as striate cortex, or V1. Division between magnocellular and parvocellular pathways persists at this level of processing as well. Color sensitive P cells in LGN project

initially to layer 4CB of V1which in turn project to layer 2 and 3 (Livingstone & Hubel, 1988). In layers 2 and 3 of V1, we find areas packed with color-responsive cells, which are given the highly technical name, "blobs" (Zeki, 1973). Blobs receive the majority of their input from layer 4CB of V1, and are therefore believed to be a parvocellular color-selective region. While color-opponent cells in blobs receive input from layer 4CB, orientation-selective cells between the blobs in this layer, called interblob regions, are thought to receive projections from either magnocellular or parvocellular pathways, and are usually unresponsive to color variations (Li & Atick, 1994). Cells in the interblob region are composed mostly of orientation selective cells that respond equally well to light of any wavelength, and due to their sensitivity to borders of figures, regardless of color, may be specialized for the analysis of form (Barrow, Bray, & Budd, 1996; Livingstone & Hubel, 1988). It is important to note that no studies show regions in V1 that are composed *exclusively* of one type of cell or another. This indicates that some cells in all regions of V1 are capable of receiving visual information from the non-dominant pathway of that region, and some cells may even be responsive to both color/form, and motion information (Livingstone & Hubel, 1988).

LGN vs. V1

Differences in response properties exist between cells in LGN and area V1, suggesting elaboration on color information from pre-cortical to cortical areas. Whereas LGN cells respond to the regions roughly defined as red-green,

and blue-yellow of the color axis, and are fit well by a sine wave, cells in V1 respond in a non-linear manner to color presentations (DeValois et al., 2000). V1 cells peak at several points across the color spectrum, as opposed to the clearer sine wave pattern of LGN cellular responses discussed earlier. There is even a slight tendency for these cells to respond preferentially to color tunings that are not common in LGN cellular response properties (DeValois, et al., 2000). This transformation of signals from LGN to V1 indicate that an elaboration process is likely taking place, allowing all colors along the visual spectrum to be represented.

Whereas the majority of LGN cellular responses to color changes are fit well by a linear sine wave, responses of a greater proportion of cells in V1 are fit much better with non-linear, exponential models. In this study, LGN cell response to color changes have a median sine wave exponent of 1.08; very close to a normal sine wave (exponent = 1.0); while V1 responses have a median exponent of 1.90; evidence of an exponential fit (DeValois et al., 2000). The difference in response properties between these two areas is attributed to the contribution of delayed S cone input. While S cone input is rarely found in cells occupying the LGN, there is nearly double the input of S cones in area V1 (DeVelois et al., 2000).

Visual Cortex Area 2 (V2)

Once again, clear division of magnocellular and parvocellular pathways exists at area V2, consistent with the separation of areas responsible for different

aspects of vision, which can be deemed color and form (parvo) vs. motion (magno). However, evidence shows the functional segregation to be less distinct. Structurally, segregation is evidenced by the existence of three distinct striped regions in V2; thick stripes, thin stripes, and pale stripes. Stripes high in concentrations of cytochrome oxidase (CO) appear relatively dark, and are either thick or thin in relative width. There are also stripes in V2 that are low in dark-colored CO, and are therefore deemed pale stripes (Hubel & Livingstone, 1987).

Further evidence of segregated functioning in V2 exists. Thick stripes of V2 are composed of higher proportion of direction-sensitive cells, and receive the majority of their input from layer 4B of V1, a magnocellular layer. Pale stripes are composed of a higher proportion of orientation-selective cells and receive their input from the interblob regions of V1, which also contains a large proportion of orientation-selective cells. Finally, the thin stripes of V2 are more densely composed of color-sensitive cells, and quite predictably, receive their input in large part from blobs in area V1.

Levitt, Kiper, & Movshon (1994) looked at the response properties and receptive fields of a sample of 213 V2 cells across all three stripe regions. Chromatic stimuli of varying luminance were presented to monkeys, in the form of red, green, blue, and yellow fields, to determine color selectivity, luminance preference, and orientation selectivity. Responses show that the majority of V2 cells generally respond better to luminance variation than to isoluminant color variation. The neurons found to be more responsive to isoluminant color variation were mostly red-green opponent cells. Moreover, 48% of these strictly

color-selective cells in V2 were found to be unresponsive to orientation, compared to 28% of typical V2 cells. Anatomical data revealed that unoriented color-selective cells were indeed clustered in thin stripe areas of V2, although this clustering was not exclusive to cells of these particular response properties. Of the 20 strictly chromatic cells they identified in their sample, 15 were localized in the thin stripe regions, and the other 5 in pale stripe regions. Again, it is important to note that although there was clear evidence that color-selective unoriented cells clustered in the thin and pale stripes of V2, all types of cells could be found in all stripe areas.

Chromatic Properties: V1 vs. V2

One of the main foci of Levitt et al. (1994) was to determine differences in response properties of cells in V1 and V2. There is some evidence to support the binding of different aspects of visual image in area V2. As mentioned earlier, DeValois et al. (2000) attempted to fit sine wave models to response properties of cells in LGN and V1 and found that while cells responses in LGN could be described relatively well by linear models, cells in V1 were better described by exponential models. Likewise, combination of cone inputs for cells in V2 led to even less model linearity than cells in V1, indicating either an even more narrow tuning for individual colors, or an equal response across the color axis, than cells in V1.

Of particular interest was the difference between V1 and V2 in regard to cell selectivity. It was noted earlier that although cells in specific areas could be

characterized generally, there were cells in all areas that were not of the majority (i.e. orientation-selective cells in the color-selective blob areas). This held true in this study of V2 to an even greater degree than in studies of V1. The authors even note that the most striking aspect of V2 they found was its homogeneity across different CO stripes (DeValois, 2000; Levitt et al., 1994). It appears, based on the results, that parvocellular pathway and magnocellular pathway convergence occurs progressively more in the higher cortical areas than early in the visual system.

Clearly, there is segregation between magnocellular and parvocellular pathways at all levels of visual processing. However, given that we experience vision holistically, binding of the component parts of a visual image must take place somewhere along the neural pathway associated with vision. Information proceeds through the various anatomical structures associated with vision, the distinct functions of magnocellular and parvocellular divisions, though still identifiable, become less exclusive. Neuronal response properties become more homogenous and areas become more functionally integrated from the retina, to LGN, to areas V1 and V2 of the visual cortex, allowing the human visual system to experience the wonderful world of color.

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