A Biologically Plausable Neurodynamical Model of Color & Form in the Primary Visual Cortex

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Abstract

We present a computational model of the primary visual cortex (V1) inspired by current neurobiological understanding. This understanding treats color and shape as intrinsically connected and, as a consequence, predicts perceptual phenomena such as color induction and assimilation to arise very early in visual processing. We incorporate this understanding into a dynamical model of neuronal activity responding to static or dynamic visual stimuli. Our model confirms the psychophysical predictions on a range of experiments, offering credence to the biological theories.

Index Terms

primary visual cortex, striate cortex, V1, receptive field, single opponent, double opponent, color assimilation, color induction

I. INTRODUCTION

COLOR induction and contrast are two related, opposing, perceptual phenomena. The former is a change in perceived color "toward" a nearby color, while the latter is a change of one color "away" from the nearby color. Neurophysiological research suggests that these phenomena may arise as early in primate vision as the primary visual cortex (V1). It is proposed that the boundaries between two colored regions drive these effects. Specifically, research in the field describes neurons which fire selectively to boundaries between certain colors, so called double opponent cells, and identifies them as being critically related to the color perceived.

Within, we propose a computational model designed around the current understanding of this biology. We present two implementations, one more biologically accurate, and another more computationally elegant. We explore the behavior of these models with respect to what they can teach us about the assumed biological theories, as well as their application to the field of computer vision.

II. STATE OF THE ART

A. Neurobiology

Historically, it was widely believed that color and shape are two distinct aspects of visual perception. Truly, this line of though is intuitive: one can perceive the color of a flat surface which occupies our full field of vision, despite its lack of 'shape', likewise we can see the shape of achromatic objects, as in black and white film. This theory of perception innervated neurophysiological understanding and was supported by neurobiological findings, such as that the lateral geniculate nucleus (LGN), the pathway which carries information from the retina to the primary visual cortex (V1), consists of three entirely distinct layers; two (the parvicellular and konicellular) carrying only color information, and one (the magnocellular) dealing purely in achromatic contrast (edge) information. Based on early anatomical observations, it was proposed that these three LGN pathways for color and contrast are then processed into two separate streams in V1, one for color and the other for form. This separate handling of color and form indicated to researchers that, as suspected, these two perceptual concepts are, indeed, processed separately in the brain.

Research in the past decade or so has seen a shift from this thinking, however. Psychophysical observations, such as those in Figure 1, influenced researchers to consider that color and form are more intrinsically related than previously thought. In these examples, we see that the perceived color of the inner square is highly dependent on the background and, most importantly, how the inner square *contacts* the background. The color perceived is not just determined by the physical properties of the surface, but also by the context in which the surface is viewed. Furthermore, we can observe that this contextual influence comes largely from the boundary edges of the surface: in example (c), the dulling color assimilation effect witnessed in (b) is almost entirely negated by simply adding a thin border. That is, by removing contact between the inner square and the background, the effect of the context is significantly reduced. In fact, "the color appearance of a region may be more dependent on color contrast at the boundary of the region than it is on the spectral reflectance of the region's interior." [1, p.572]
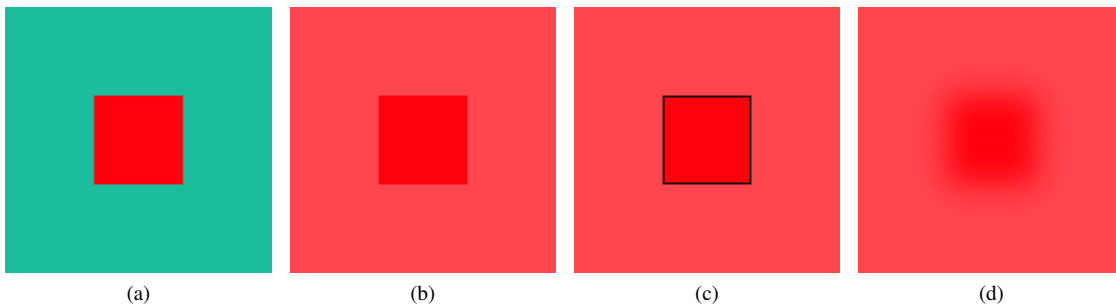
Fig. 1. Psychophysical example emphasizing the effect of edge contrast in color perception. In all cases, the center square is the same physical color. On (a) the green background, however, it appears much brighter than it does on (b) the red background. (c) Adding a thin black border negates the assimilation effect, increasing the perceived brightness of the center square. (d) Blurring the background, on the other hand, seems to enhance assimilation, lowering the perceived brightness at the center.

With these psychophysical observations in mind, much research has been focused on the specific neurobiological mechanisms behind the perception of color. The current view holds that while the LGN does indeed carry color and contrast information through distinct pathways to the striate cortex (V1), once there, it is now thought that color and form become deeply intertwined as they are processed further. To explain the simultaneous processing of color and form in V1, the literature proposes two broad classifications of neurons: single opponent cells, & double opponent cells (Johnson et al. Color and Orientation in V1).

Opponency, in neurobiology, refers to antagonistic inputs to a neuron: one source of input exciting the neuron, while another source inhibits it. If the two sources provide equal input, for example, they would cancel out and the neuron would not fire. With respect to cells in the early visual system, we are here specifically referring to chromatic and spatial opponency, as will be detailed below. Briefly, single opponent cells respond best to large areas of color, while double opponent cells respond only to the boundaries between such areas.

Single Opponent Neurons

Single opponent neurons are built using the classical center/surround receptive fields. The ON receptive field exciting the cell when presented with a particular color in the center, the OFF receptive field exciting the cell when another color is *removed* from the surround.

　// TODO *add image of simple behavior: gradient response to isoluminant chromatic boundary*

　// TODO *add image of simple behavior: no response to intensity changes*

　// TODO *add image of ON/OFF differences: R-G cell responds to fullscreen green light removed (not red removed)*

(a) Symmetric Balanced　　　　　　　　(b) Symmetric Unbalanced　　　　　　　　(c) Center/Surround
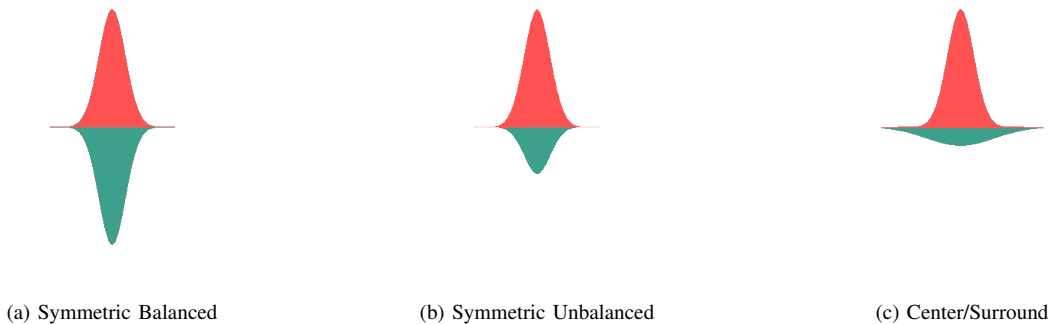
Fig. 2. Visualization of a variety of single opponent (SO) receptive fields.

Achromatic Single Opponent Neurons: Sometimes called non-opponent cells, they have no chromatic nor spatial opponency. Instead, they amalgamate all color input in a balanced manner so as to only respond to changes in luminosity. Technically, we can consider non-opponent cells to be a special case of single opponent cells.

　// TODO *are NO cells the same as SO cells? What about achromatic double opponent cells?*

　// TODO *add image depicting example receptive field(s)*

　// TODO *add image of simple behavior: gradient response to ((mono)chromatic) intensity changes*

　// TODO *add image of simple behavior: no response to isoluminant chromatic boundaries*

Double Opponent Neurons

　Point: Double opponent neurons are edge detectors.

Story: Double opponent neurons are a topic of confusion in the field of neurobiology. All researchers on the topic seem to agree that the input to the neuron is that of two single opponent neurons itself. In this sense, the term "double opponent" can be thought of as indicating that the dimensionality of color opponency has been doubled. However, another camp of researchers take the definition a step further and suggest that the two SO inputs are spatially offset. By this definition, the term "double opponent" is thought to indicate that the cell is sensitive to opponency in two *different* dimensions, color and space.

The distinction is non-trivial as the response patterns differ, and thus the interpretation of their role in vision differs.

// TODO present the differences between the two DO configurations

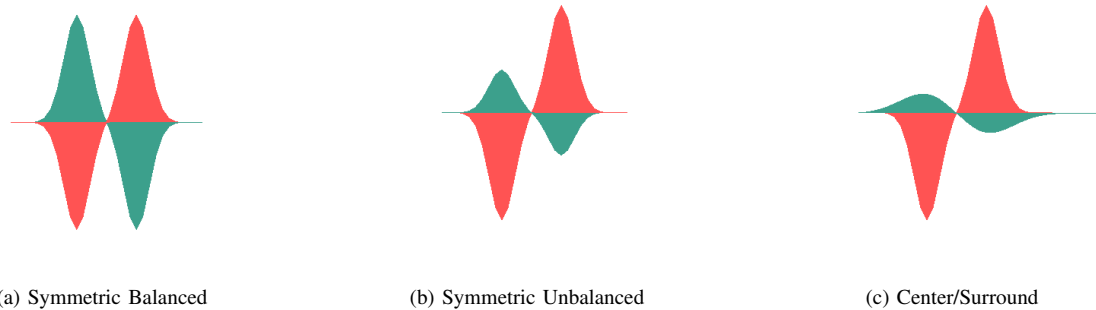(a) Symmetric Balanced　　　(b) Symmetric Unbalanced　　　(c) Center/Surround

Fig. 3. Visualization of a variety of double opponent (DO) receptive fields.

Orientation Selectivity: Research shows that cells identified as double opponent are orientation selective. That is, they respond most strongly when stimulated by a border of particular orientation, less so with variation from that preferred orientation, and weekly, if at all, to borders orthogonal to the preferred orientation. This is intuitive given the organization of the receptive field as previously defined.

// TODO describe Orientation Selectivity

// TODO *add image depicting example receptive field(s)*

// TODO *add image of simple behavior: peak activity AT sharp edge*

Spatial Frequency Selectivity: It is recognized that

Achromatic Double Opponent Neurons: **// TODO describe achromatic double opponent cells**

// TODO *add image of Shapley response curves for NO, SO, & DO*

// TODO *mention relative abundance of NO, SO, & DO*

To recapitulate: single opponent neurons fire best to full field stimulation while double opponent neurons fire only at the boundaries between particular colors. Both cell types can be found in color preferring and achromatic flavors.

B. Computational Modeling:

The model described in this research is an extension of that presented by Penacchio *et al.* [2], itself based on work by Z. Li [3], [4]. Before detailing our implementation, it is important to review prior art, these works and others. As our goal is to model the behavior of color preferring and achromatic single opponent and double opponent neurons, we will also review other computational endeavors tackling the issue of color and/or form from a biologically inspired perspective.

Li's Neurodynamical Model for Segmentation (1999)

In Li's original work, a neurodynamical model was presented which focused on the global region segmentation using only local interactions between neurons. In the interest of simplicity, Li's implementation dealt only with the nature of these interactions, ignoring where the stimulus, or information, might be coming from. Conceptually, Li defined neurons by the physical position in the image and the 'feature' to which they are sensitive. She then defined the connections between these neurons such that those physically close to each other, and sensitive to similar features, interacted most strongly. Stimulation of one neuron, then, positively stimulated (excited) similar neurons nearby, and negatively stimulated (inhibited) dissimilar neurons nearby. Such excitation and inhibition cascades through the network naturally, producing a large scale response pattern defined by local stimuli.

In the model presented, Li used oriented bars as features, though expressed that any logical feature could be reasonably considered in its place. This choice was biologically inspired by neurons sensitive to specifically oriented bars, the aforementioned double opponent cells. When considering such features, inter-neuronal connections can be logically deduced: two neurons positively interact most when both 1) are sensitive to similarly oriented bars and 2) are co-located along that same orientation. Two neurons negatively interact most when either of these two conditions is not met.

//TODO *include graphic or oriented bars which positively & negatively interact*

By defining the neuronal connectivity in this manner, patterns of neurons sensitive to co-located and co-aligned bars positively interact with each other to enhance their collective response to the stimuli. Similarly, isolated stimuli negatively interact with their neighbors and are silenced. From these local interactions, global features are enhanced if they satisfy the neuronal connectivity rules, and noise is suppressed. Li showed that this method can be used to enhance contours and identify boundaries between regions for which normal segmentation methods struggle.

Penacchio, Otazu, & Dempere-Marco's Neurodynamical Model for Brightness Induction (2013)

Li's work laid the foundation for Penacchio *et al.* who extended the model to a usable framework which:
1) Uses real black & white images /movies as input.
2) Utilizes discrete wavelet transforms to extract edges (more on this later).
3) Added multi scale support.
4) Summarizes the results into an output 'perceptual image'.

Their research was focused on observing brightness induction (BI) arising from such a neurodynamical model.
- No color, just black & white *edges*
- Generalized to real images (edges vs lines)
- Added scales
- Dynamical processing
- **Avoid detail, save that for *Method*..?**
- Extension of Z. Li's edge detection work
- Uses DWT to extract oriented edges in grayscale
  - ..in our context, it's essentially a luminence sensitive double opponent cell.

Itti, Koch, & Niebur's Model for Saliency (1999)

- Opponent color transformations
- No double-opponent cells
- Center & surround using scales
- Has scales, but collapses them into one (right?)
- *No dynamical processing*

Zhang, Barhomi, & Serre's Biologically Inspired Color Descriptor (2013)

- Single & double opponent color using weights
- Has center/surround (Gabbor filters for DO, gaussians for SO?)
- No scales
- *No dynamical processing*

Spitzer & Barkan's Model of Color Induction (2005)

- Single & double opponent color transformations using receptive fields
- Center & surround receptive fields
- *No dynamical processing*

Comparison of Models

These models, though approaching different problems in different ways, can be compared to each other in terms of our current work. In Table I we contrast and compare the features of the presented computational models with respect to ours.

// TODO *describe what exactly qualifies for 'colors', 'scales', and 'orientations' in this general comparison*

// TODO *add citations to Table I*

	Li [4]	Penacchio [2]	Itti	Zhang	Spitzer	Connolly
Dynamical	Y	Y	N	N	N	Y
Colors	N	N	Y	Y	Y	Y
Scales	N	Y	Y	N	N	Y
Orientations	Y	Y	Y	N	N	Y
SO	N	N	Y	Y	Y	Y
DO	N	Y (achromatic)	Y	Y	Y	Y
SO RF	N/A	N/A	Gaussian Pyramid	None	Gaussian	Gaussian / DWT
DO RF	N/A	DWT	Gaussian Pyramid	None	Gabor	Gabor-like / DWT
Goal	Saliency	Brightness Induction	Saliency	Descriptor	Color Induction	Color Induction

TABLE I

COMPARISON OF SOME OF THE RELEVANT MODELS. EACH HAS VERY DIFFERENT GOALS, AND THUS TAKES A VERY DIFFERENT APPROACH. SOME INCLUDE COLORS WHILE OTHERS DON'T. SOME ARE DYNAMICAL WHILE OTHERS AREN'T.

To summarize, the purpose of this project is to **feed opponent color information into a neurodynamical model** sensitive to edges & surfaces in a biologically inspired manner.

// TODO *We need to properly summarize the State of the Art before proceeding.*

- What does the biology predict?
- What have computational models done?
- Where do computational models fall short? (A: no dynamical color model)
- Thus, where does our work fit into the field?

III. METHOD

We present a computational model designed to be representative of the aforementioned biology. The implementation of this model can be conceived of as two distinct parts:

1) The transformation of raw image data into a biologically meaningful information representation.
2) The dynamical processing of this information in accordance with neurobiological theory.

Computational Representation of Visual Information

The response behavior of both single opponent and double opponent cells is modeled. In both cases we model color preferring and achromatic cells.

The issue of how represent information meaningfully can itself be broken down into two issues: color opponency, neural receptive fields.

Color Opponency: With only three cone cells, the brain perceives the gamut of colors we see by comparing and contrasting their stimuli. This is known as the opponent color theory. In modeling vision meaningfully, it is important to consider color information in this way.

Single opponent (SO), and double opponent (DO) cells comprise the focus of our modeling efforts. SO cells respond to surfaces while DO cells respond to the boundaries between surfaces.

TODO How is the data represented in V1?

TODO Introduce the 2 data transformations and their respective meanings

1) RGB $\rightarrow$ receptive fields $\rightarrow$ LDRGBY
2) RGB $\rightarrow$ L*a*b* $\rightarrow$ DWT

- In either case, it's then transformed into neuronal excitation (scale 1-4) and used as the INITIAL STIMULUS for each time step.

A. Opponent Processing of Neural Receptive Fields

RGB $\rightarrow$ receptive fields $\rightarrow$ LDRGBY

The color opponent theory defines three axes visual information, obtained by processing of cone activity from the retina. These axes are Red-Green (R-G), Blue-Yellow (B-Y), and Light-Dark (L-D).

The pathways from the retina through to V1 inform us that color sensitivity and luminance sensitivity in V1 derive from the various combinations of input from L, M, and S cones in the retina. We compute such transformation based on work by L. Itti *et al.* [**?**]. We extend their equations so as to integrate surround effects at this low level, rather than simply calculating color opponency at the pixel level. We redefine their equations as such, where *r*, *g*, and *b* are the red, green, and blue components of the image, respectively, and where *c* and *s* define the center and surround convolutions, respectively.

$$R(c, s) = max(0, r(c) - \frac{g(s) + b(s)}{2})$$
$$G(c, s) = max(0, g(c) - \frac{r(s) + b(s)}{2})$$
$$B(c, s) = max(0, b(c) - \frac{r(s) + g(s)}{2})$$
$$Y(c, s) = max(0, \frac{r(c) + g(c)}{2} - |\frac{r(s) - g(s)}{2}| - b(s))$$

Where *c* indicates the 'center' and *s* indicates the surround, used to define the relationship between center and surround receptive fields. For example, *c* can be given a smaller receptive field and greater weight than *s*. Centers and surrounds are built by applying gaussian filters to the raw image channels. This simulates a neuron at V1 receiving input from many cones.

// TODO *show diagram of single opponent center & surround*

We also introduce two new opponent channels, lightness (L) and darkness (D):

$$L(c) = max(0, \frac{r(c) + g(c) + b(c)}{3})$$
$$D(c) = |min(0, \frac{r(c) + g(c) + b(c)}{3})|$$

It's important to note that the L & D components do not incorporate surround effects as the color opponent channels do. More work can be done in this regard.

Information from the retina is transduced to opponent color information by contrasting stimulus of cones of different wavelength sensitivity. To model visual information in V1, we apply this opponent color processing to raw image data. Figure **??** depicts some of the opponent receptive fields we modeled.

Double opponent cells are constructed exactly as single opponent cells by defining off-center receptive fields.

// TODO *show diagram of double opponent center & surround*

Considerations:

- CON: Relatively slow
  - Could be improved with Gabor instead of gaussian for DO cells.
  - It's just an upfront cost, the neurodynamical processing is the most expensive.
- PRO: more receptive field control (explicit RF definitions)
- CON: requires tweaking of receptive fields
- PRO: more true to biology (combination of signal rather than numeric transformation of color space)
- CON: requires decision on meaningful RGB combination (should be elucidated from biology)
  - Pre-transformation to LMS might be valuable/meaningful.

// TODO *show original & decomposed image*

B. Discrete Wavelet Transform in Opponent Colorspace

RGB → L*a*b* → DWT

Previous work by Penacchio *et al.* [2] utilized a discrete wavelet transform (DWT) to decompose a greyscale image into its oriented edges at scale. In the context of our research, this could be thought of as representing achromatic double opponent cells; the response is greatest at luminosity boundaries, and nonexistent on surfaces or at chromatic changes. In this work we extend their approach to the opponent color space and examine it's applicability as a replacement of the aforementioned explicit opponent processing of neural receptive fields.

Process:

- Convert image from RGB to L*a*b*
- Subtract 50 from L* to center it on 0 (a* and b* are already zero centered)
- Apply DWT at each scale
1) the wavelet signal at each scale is the DO response in that channel
2) the wavelet residual at each scale is the SO response in the channel
- To recover R, G, B, Y, L, & D we take positive and negative values of the R-G, B-Y, & L-D channels.

This implementation comes with obvious deviations from the biology:

1) By transforming RGB to L*a*b* at the pixel level, we lose receptive field integration
2) The brain doesn't translate to opponent colors and then find edges
   - this can be formalized as the difference between
     a) the addition of convolutions
     b) the convolution of additions

What are the advantages?

1) Computationally efficient & relatively fast
2) ...?

// TODO *show diagram of oriented DWT filter*

// TODO *show original & decomposed image*

Neurodynamical Processing

We've described two processes for transforming raw data into reasonable input to the neurodynamical model. The two have their pros and cons, but both are applicable. In either case, the chromatic and achromatic SO and DO information is used as input, conceptually, neural stimulation. The model then processes the dynamical interactions between the neurons in order to propagate contextual effects where applicable.

Notes:

- An extension of X. Otazu's PLoS One model
  - itself an extension of Z. Li's 1999 model
- describe what exactly 'neurodynamical' means
- describe how the X. Otazu & Z. Li models work and are extended
- describe how this is agnostic to the initial transformation (data is cell firing rates (1-4))

IV. EXPERIMENTS

1) Analyze Data Transformation:

- Opponent Receptive Fields
  - does SO behave as expected
  - does DO behave as expected
  - does Itti space behave as expected
- DWT
  - does SO behave as expected (as Itti?)
  - does DO behave as expected
  - (L*a*b* is trusted)
- What are the differences between these outputs?
  - Show side by side LDRGBY/LAB+- convolutions
- What are general shortcomings?
  - OFF receptive fields function in time: removing green excites red. Our RFs don't reflect this.

2) Analyze Neurodynamical Model:

- We can trust the concept because of Otazu 2013
- We need to analyze how color works
  - Connections between color channels
    * What are our assumptions? (& why?)
    * How does it modify the results over no connections?
    * How does it modify the results over full connections (including between opponents)?
  - Connections between SO and DO

V. RESULTS

TODO

VI. CONCLUSIONS

TODO

APPENDIX A
APPENDIX TITLE

TODO

ACKNOWLEDGMENT

The authors would like to thank...

NOTES

State of the Art - Biology - Notes:

1) What is color?
   - Subjective
   - Correlates to reflectance patterns
2) Historical view → separation of color & shape
   - Parallel/modular/segregated processing [1]
   - Intuitive
     - Black & white movies work fine (Shapley 2011)
     - Full field color can be seen fine
     - LGN research suggested parvicellular & konicellular has color, magnocellular has contrast (edges)
     - Similarly, V5 was 'motion'
3) Current view → integration of color & shape
   - All information is processed as one information stream (too strong??)
   - Color opponency
     - Discuss LMS & opponent color theory
     - Retinal receptive fields & horizontal cells
     - LGN information reflects opponent colors (no spatial opponency)
     - SINGLE OPPONENT CELLS RESPOND BEST TO FULL FIELD COLOR
   - Spatial opponency
     - LGN information upgraded to include spatial opponency
     - Double opponent cells: color & spatially opponent
     - Spatial frequency sensitivity
     - Orientation sensitivity
     - Shapley shows most V1 cells are double opponent
     - DOUBLE OPPONENT CELLS RESPOND BEST TO COLOR BOUNDARIES
   - DO & SO roles
     - If there are SO cells in V1, they aren't just a stepping stone, but encode valuable information. Thus, they likely work in concert with DO cells (more numerous (Shapley))
     - DO cells detect edges → saliency? (Z. Li)
   - Interactions (hypercolumns, CO blobs, etc.)
     - Not well understood =(
     - Retinoisotopic
     - Hypercolumns (Z. Li?)
     - What does Shapley think of CO blobs (youtube Q & A)?

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