

Introduction of a Biologically Plausible Color Descriptor to a Neurodynamical Model of the Primary Visual Cortex

Sean Thomas Connolly

Abstract

We present a computational model of color description & processing in the primary visual cortex (V1), inspired by current neurobiological understanding. This understanding posits single and double opponent neurons as fundamental to low level color processing. We offer a novel representation of color by defining these cells' responses and the connections between them, within the framework of a dynamical model of neuronal activity. Our model reproduces perceptual experiences in a number of cases, offering credence to said 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

// **TODO** This understanding treats color and shape as intrinsically connected and, as a consequence, predicts perceptual phenomena such as color induction to arise very early in visual processing.

Historically, it was widely believed that color and shape are two distinct aspects of visual perception. Truly, this line of thought 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 parvocellular and koniocellular) 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 confirmed for researchers that, as suspected, these two perceptual concepts are 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 devoted to elucidating the exact 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, 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 of information: one source of input excites the neuron, while another inhibits it. If the two sources provide equal input, for example, they would cancel out and the neuron would not fire. *furthermore, the removal of an antagonist can excite!* 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. This other color is called its opponent, and thus colors come in opponent pairs. In the human visual system, we recognize three axes of color opponency: red vs. green, blue vs. yellow, and light vs. dark. To construct such concepts of color from the three cones we possess, limited in their ability to discriminate stimuli, ..? By contrasting relative activity with neighboring cones, the retina can construct signal representative of psychological concepts of color.

// 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)

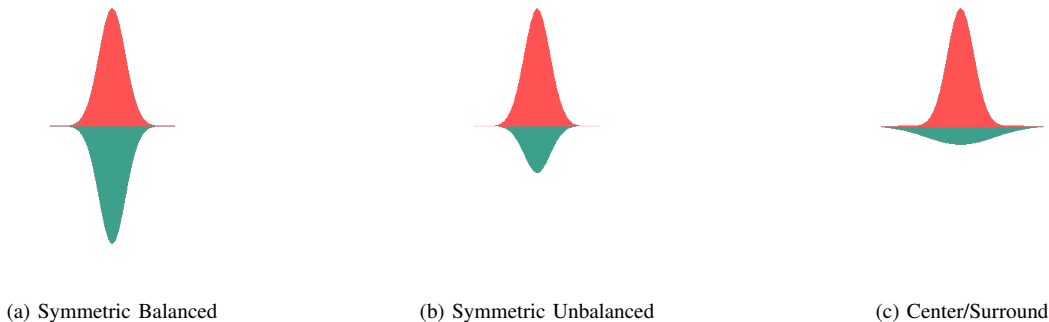


Fig. 2. Visualization of a variety of single opponent (SO) receptive fields.

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

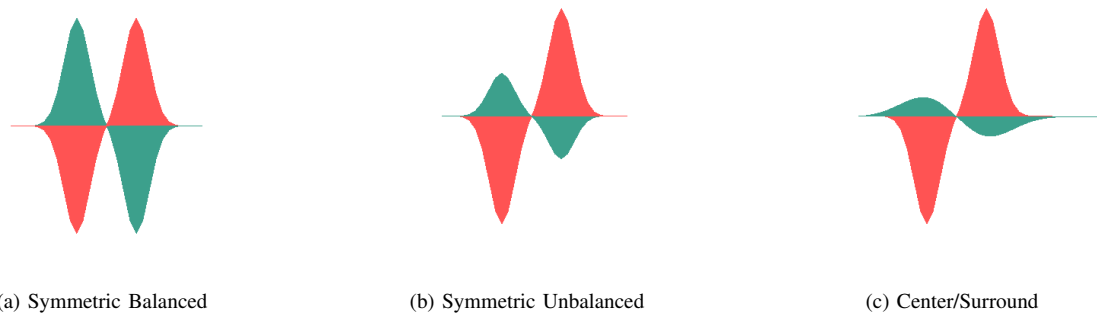


Fig. 3. Visualization of a variety of double opponent (DO) receptive fields.

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 (Gabor 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

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

- *Description of Visual Information*: transformation of image(s) into a biologically meaningful representation.
- *Neurodynamical Processing*: iterative processing of the dynamic interactions between the neurons modeled.

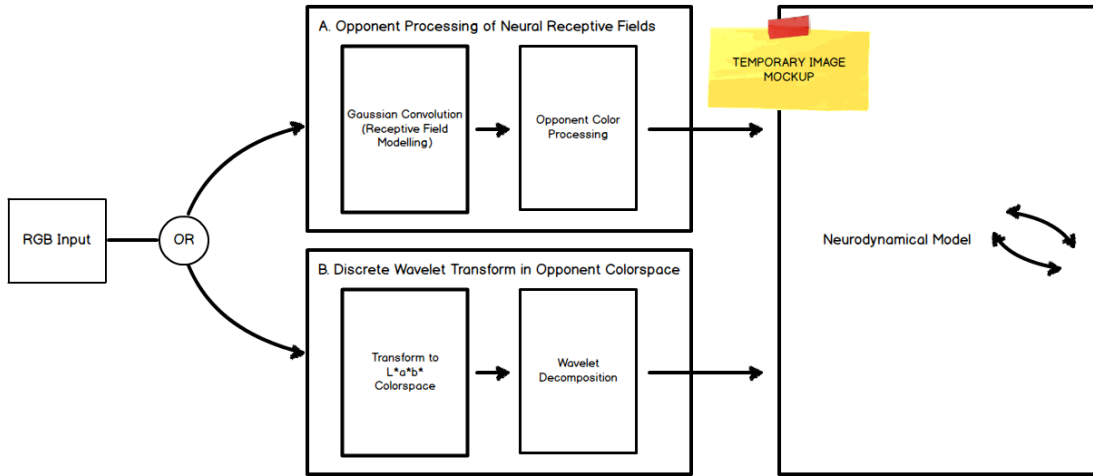


Fig. 4. High level schematic of model components. The point of emphasis here is that neurodynamical model is agnostic to how the data is processed upfront, as long as the format is correct. The two methods for data preparation (read: color description) are independent of each other and analyzed separately.

Description of Visual Information

The opponent-process 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). Neurobiological research corroborates such processing of color information (// **TODO** cite this). // **TODO MORE ON OPPONENT-PROCESS THEORY**

// **TODO** PARAGRAPH ON SINGLE AND DOUBLE OPPONENT CELLS

In accordance with this understanding of biology, the image transformation process should 1) separate opponent color components from each other, and 2) separate surface information from boundary information. We describe two different approaches to this end. The first approach, herein referred to in proximity as the "*Opponent Processing of Neural Receptive Fields*", represents an effort to explicitly transform raw visual data in strict accordance with neurobiology. Essentially attempting to mimic the information processing pathways of the retina, lateral geniculate nucleus (LGN), and striate cortex (V1). The second approach, termed with equal verbosity, is the "*Discrete Wavelet Transform in Opponent Colorspace*". Here we stray from the details of the biological pathways in an attempt to achieve the same end, through more computationally efficient means.

In both, the input is a normal RGB image, and the output to the neurodynamical model is a 5 dimensional matrix containing 6 opponent color channels (R, G, B, Y, L, & D), each deconvoluted into its surface and oriented edge components, and 1 or more scales. In this work we generalize oriented edges into 3 orientations: horizontal, diagonal, & vertical. Before processing by the neurodynamical model, this data is normalized so as to circumvent differences between the data output by these two methods.

A. Opponent Processing of Neural Receptive Fields

1) *Single-Opponent Neurons*: Processing starts by convolving each of the L, M, and S cone spectral response functions with two different, concentric, centered, circular gaussian filters. These convolutions simulate integration of information in a neuron's receptive field. One convolution is used to build the center of a cell's receptive field, the other convolution, the surround. In a classical center-surround configuration, the center is smaller and weighed significantly more heavily than the surround, as in Figure 2 (c).

In our implementation, for convenience, we utilize the R, G, and B channels of the raw image as an approximation of L, M, and S cone activity, respectively. It should be noted that a preprocessing step could be performed to better match RGB to LMS so as to be more biologically consistent. The impact is likely negligible.

To construct opponent color channels, we contrast center (c) and surround (s) convolutions of the L, M, and S channels into three pairs: two color [?] and one achromatic.

$$R(c, s) = \max(0, L(c) - M(s)) \quad (1)$$

$$G(c, s) = \max(0, M(c) - L(s)) \quad (2)$$

$$B(c, s) = \max(0, S(c) - \frac{L(s) + M(s)}{2}) \quad (3)$$

$$Y(c, s) = \max(0, \frac{L(c) + M(c)}{2} - S(s)) \quad (4)$$

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

$$L(c, s) = \max(0, \frac{L(c) + M(c) + S(c)}{3} - 0.5) \quad (5)$$

$$D(c, s) = |\min(0, \frac{L(c) + M(c) + S(c)}{3} - 0.5)| \quad (6)$$

// **TODO** consider $\frac{L(c)+M(c)+S(c)}{3} - \frac{L(s)+M(s)+S(s)}{3}$

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

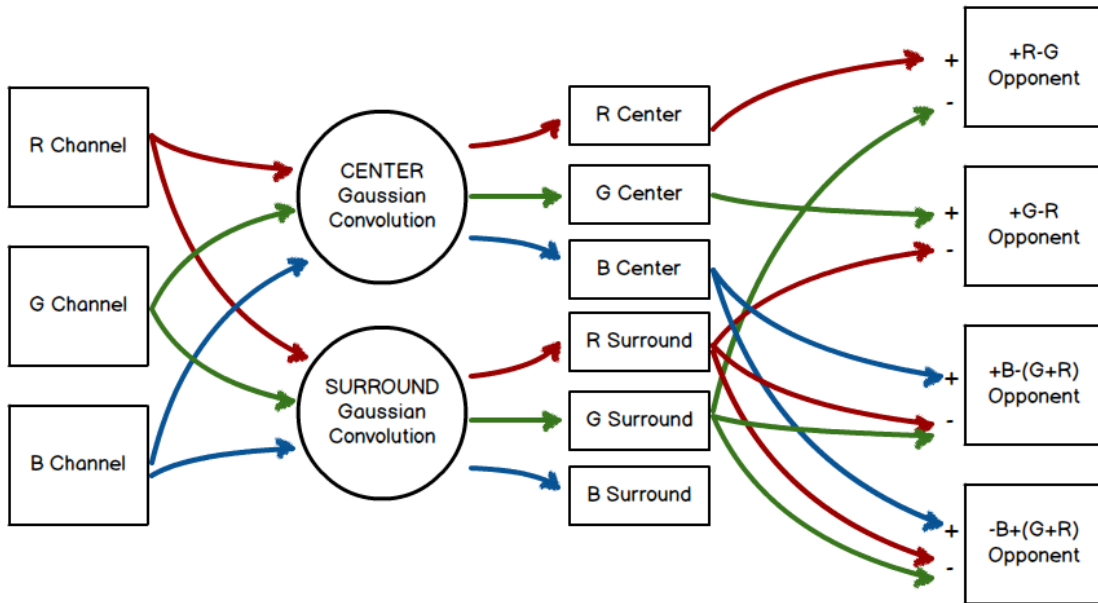


Fig. 5. Depiction of opponent processing of center/surround receptive fields. The RGB channels are convoluted with gaussians and then combined to obtain opponent color signal.

// **TODO** ADD L & D to Figure 5

2) *Double-Opponent Neurons*: The process of constructing double-opponent color channels is exactly the same as in *Single-Opponent Neurons* above, the only difference being the definition of the gaussian filters used to define the cells' receptive fields. Instead of using two concentric, centered, circular gaussian filters, for double-opponent cells we use asymmetrical, off-center, elongated gaussian filters, like those depicted in Figure 3. As with the single-opponents cell model, the 'center' and 'surround' (more appropriately referred to as 'excitatory' and 'inhibitory' in the context of double-opponent cells) receptive fields can be adjusted to different sizes, shapes, and weights each. For our tests we worked with symmetric balanced receptive fields, as in Figure 3 (a).

// **TODO** reference 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

$RGB \rightarrow L^*a^*b^* \rightarrow DWT$

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 current 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 its applicability as a replacement of the aforementioned opponent processing of neural receptive fields.

// **TODO** PARAGRAPH ON LAB OPPONENT COLOR SPACE

// **TODO** PARAGRAPH ON DISCRETE WAVELET TRANSFORM

// **TODO** FIGURE: show diagram of oriented DWT filter

// **TODO** FIGURE: show original & decomposed image

// **TODO** PARAGRAPH ON INTERPRETATION OF COMPONENTS (DO & SO)

// **TODO** PARAGRAPH ON WORKFLOW: $RGB \rightarrow L^*a^*b^* (-50) \rightarrow DWT \rightarrow ON/OFF$

// **TODO** PARAGRAPH ON PROS/CONS

1) Notes: 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) ...?

Neurodynamical Processing

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

// **TODO PARAGRAPH ON RETINOISOTOPIC** ($X_{i\gamma\sigma\theta}$)

The model processes input in a retinoisotopic manner. That is, neurons are laid out in physical corresponde

// **TODO PARAGRAPH ON MULTIPLE FEATURES AT EACH POSITION** (hypercolumn of $\gamma, \sigma, \&\theta$)

// **TODO PARAGRAPH ON INTERACTION MAPS** (J & W)

// **TODO PARAGRAPH ON** γ

// **TODO PARAGRAPH ON** σ

// **TODO PARAGRAPH ON** θ

$$\left\{ \begin{array}{l} \dot{x}_{i\gamma\sigma\theta} = -\alpha_x X_{i\gamma\sigma\theta} \\ \quad - g_y(y_{i\gamma\sigma\theta}) \\ \quad - \sum_{\gamma' \neq \text{opp}(\gamma), \Delta_\sigma, \Delta_\theta \neq 0} \Psi(\gamma', \Delta_\sigma, \Delta_\theta) g_y(y_{i\gamma\sigma + \Delta_\sigma\theta + \Delta_\theta}) + J_0(g_x(X_{i\gamma\sigma\theta})) \\ \quad + \sum_{j \neq i, \gamma', \sigma', \theta'} J_{[i\gamma\sigma\theta, j\gamma'\sigma'\theta']} g_x(X_{j\gamma'\sigma'\theta'}) \\ \quad + I_{i\gamma\sigma\theta} \\ \quad + I_0 \\ \dot{y}_{i\gamma\sigma\theta} = -\alpha_y Y_{i\gamma\sigma\theta} \\ \quad + g_x(X_{i\gamma\sigma\theta}) \\ \quad + \sum_{j \neq i, \gamma', \sigma', \theta'} W_{[i\gamma\sigma\theta, j\gamma'\sigma'\theta']} g_x(X_{j\gamma'\sigma'\theta'}) \\ \quad + I_c \end{array} \right. \quad (7)$$

// **TODO PARAGRAPH ON OTHER PARAMETERS** (eg: I_c)

2) 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

3) *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.

4) *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/segreated processing [1]
 - Intuitive
 - Black & white movies work fine (Shapley 2011)
 - Full field color can be seen fine
 - LGN research suggested parvicellular & koniocellular 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 =(
 - Retinotopic
 - Hypercolumns (Z. Li?)
 - What does Shapley think of CO blobs (youtube Q & A)?

REFERENCES

- [1] Shapley, Robert, Michael Hawken, and Elizabeth Johnson. *Color in the Primary Visual Cortex*. The Visual Neurosciences. Vol. 2. Cambridge, Mass.: MIT, 2004. 568-86. Print.
- [2] Olivier Penacchio, Xavier Otazu, and Laura Dempere-Marco. *A Neurodynamical Model of Brightness Induction in V1*. PLoS ONE 8.5 (2013): E64086. Web.
- [3] Zhaoping Li. *A Neural Model of Contour Integration in the Primary Visual Cortex*. Neural Computation 10.4 (1998): 903-40.
- [4] Zhaoping Li. *Visual Segmentation by Contextual Influences via Intra-cortical Interactions in the Primary Visual Cortex*. Network: Computation in Neural Systems 10.2 (1999): 187-212.