Color-opponent mechanisms for local hue encoding in a hierarchical framework

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Abstract

Various aspects of color have been extensively studied in science and the arts for the simple reason that it conveys information and attracts attention. In perception, color plays an important role. It helps in tasks such as object recognition. In humans, color perception starts with cones in the retina. Studies in the primary visual cortex show opponent mechanisms for color representation. While single-opponent cells encode local hue, double-opponent neurons are sensitive to color boundaries. This paper introduces a biologically plausible computational model for color representation. We present a hierarchical model of neurons that successfully encodes local hue. Our proposed model benefits from studies on the visual cortex and builds a network of single-opponent and hue-selective neurons. We show that our model hue-selective neurons, at the top layer of our network, can achieve the goal of local hue encoding by combining inputs from single-opponent cells, and that they resemble hue-selective neurons in V4 of the primate visual system. Moreover, with a few examples, we present the possibility of spanning the infinite space of physical hues from the hue-selective neurons in our model.

Keywords — Single-opponent, Hue, Hierarchy, V4 neurons

1 Introduction

Artists and designers use color to convey information, moods, and structure. Moreover, color is usually employed for visual enhancement and attracting attention. The presence of color helps in tasks such as visual search and object recognition simply because color carries information and helps in identifying otherwise indistinguishable instances. In other words, in absence of color, ambiguities may arise. For example, in Figure 1, two different colors\(^1\) are shown, which have the same grayscale values. In this example, two colors with RGB values (192, 192, 64) and (34, 237, 237) were converted into grayscale by the traditional RGB to grayscale conversion function used in softwares such as MATLAB (MathWorks) and OpenCV [1] given by:

\[
Y = 0.299 \times R + 0.587 \times G + 0.114 \times B,
\]

where \(R, G, B, Y\) are red, green, blue, and grayscale values respectively. The grayscale value for the two colors shown in Figure 1 is 177. As shown in this example, when color representation is collapsed into a single dimensional grayscale representation, information is lost and the two images become indistinguishable.

Due to the importance of color, various color spaces have been introduced, each an attempt to better describe color. For example, color may be defined in the RGB space, HSV, HSL, CIE XYZ, CIELAB, etc. A key feature in all these representations is that color is modeled in a three dimensional space. Studies on the human visual system also confirm that color encoding starts in a three-dimensional space with three types of cone cells, each sensitive to a certain band of wavelengths. These wavelengths, categorized according to the cone sensitivities to short, medium and long wavelengths, form the LMS color space.

Color encoding in the visual system gets more complicated in higher layers. Cones send feedforward sig-
Figure 2: Spatial profile of a single-opponent L+M- cell. The receptive field of this cells receives positive contributions from L cones and negative ones from M cones. The spatial extent of these cone cells are different and determines the mechanism for this cell. Figure adapted from [3].

Figure 3: Color map of V4 neurons in three clusters of patches (adapted from [5]).

Figure 4 demonstrates the proposed model for color representation. In what follows, the input to the model will be shown in the RGB color space, rather than LMS, for ease of interpretation to the reader. In the event that the pre-
using a linear function: linearly rectified. The linear rectification was performed hue representation. That is, the neurons in all layers are employed linear neurons in TarzaNN for modeling our local cone types.

A combination of cone responses with opposite signs result in neurons with single-opponent receptive fields in model layers LGN, V1, and V2. Note that the receptive field sizes increase, figuratively here, from one layer to the next as described in the text. The top layer of the model consists of hue-selective V4 neurons (Best seen in color).

Our model was implemented in TarzaNN [9]. We employed linear neurons in TarzaNN for modeling our local hue representation. That is, the neurons in all layers are linearly rectified. The linear rectification was performed using a linear function:

$$\phi(P) = \begin{cases} 
0, & \text{if } mP + b < 0 \\
mp + b, & \text{if } 0 \leq mP + b \leq 1 \\
1, & \text{otherwise,}
\end{cases}$$

(2)

where $P$ is neuron activity, and $m$ and $b$ are the slope and base spike rate respectively. This linear rectifier maps responses to $[0, 1]$.

The input to the hierarchical network was always resized to 256×256 pixels. The receptive field sizes, following [10], double from one layer to the one above. Specifically, the receptive field sizes we employed were 19×19, 38×38, 76×76, and 152×152 pixels for LGN, V1, V2, and V4 layers respectively.

In each layer of the network shown in Figure 4, one single cell of each type is shown in order to illustrate how the hue-selective neurons are modeled in the hierarchy. In contrast, Figure 5 depicts the network in action. That is, in this figure, each layer consists of a number of maps, each of which showing activities of neurons of a single type with their receptive fields centered at the corresponding pixel location in the image. For example, the map labeled as red in layer V4 shows the activities of model V4 neurons sensitive to the red hue with receptive fields centered at the corresponding pixels.

Stacking the maps in the model V4 layer, in the order shown in Figure 5, will result in a three dimensional array. Each column of this array can be interpreted as a cluster of hue-selective patches, with neighboring patches sensitive to related hues, similar to those observed in V4 of monkeys reported in [5]. In other words, each column forms a rainbow of patches. Moreover, the neurons within each column, just like the patches observed in [5], share the same local visual field and have largely overlapping local visual fields with those in their neighboring columns or clusters.

In order to keep our model simple and avoid second-order equations, we skipped lateral connections between neuron types. However, these are part of future development of a second-order model.

2.1 Model LGN Cells

The first layer of the hierarchy models single-opponent LGN cells. The LGN cells are characterized by their opponent inputs from cones. For example, LGN cells receiving excitatory input from L cones and inhibitory signals from M cones are known as L+M- cells. Model LGN cell responses were computed by [11]:

$$R_{\text{LGN}} = \phi(a_L(G(x,y,\sigma_L) * R_L) + a_M(G(x,y,\sigma_M) * R_M) + a_S(G(x,y,\sigma_S) * R_S)),$$

(3)

where * represents convolution. In this equation, model LGN responses, $R_{\text{LGN}}$, is computed using a linear combination of cone activities, $R_L$, $R_M$, and $R_S$, convolved with normalized Gaussian kernels, $G$, of different standard deviations, $\sigma$. The differences in standard deviations ensure different spatial extents for each cone as described in [2]. Each weight in Eq. 3, determines presence/absence and excitatory/inhibitory effect of the corresponding cone. Following [2] and [4], the weights used for model LGN cells are shown in Table 1. As an example, consider the weights for L+M- cells. These neurons receive equal but opposite contributions from L and M cones, while S cones with weight 0 exhibit no contribution. Figure 2 depicts an example of the spatial profile of single-opponent L+M- cells. In this example, L and M cones have excitatory and inhibitory effects respectively, while S cones are absent with no effects. In total, we modeled three different LGN neuron types, L+M-, L-M+, and S+(L+M)-. Johnson et al. [4] observed that for most studied neurons, the contributing weights from S cones were weak. In this work, we sufficed to modeling $S + (L + M) -$ neuron types in order to include neurons with contributions from S cones.
Figure 5: An example showing each layer of the hierarchical color model on an image with red, green, blue, yellow regions. The neuron type is written next to each square. First, the input image is converted into LMS channels. The channels are shown as L, M, and S, from left to right. Each square in the model layers represents an array of a neuron type. The receptive field of each neuron in these arrays is centered at the corresponding pixel location. The neuron responses are shown in grayscale, with no response as black, and maximum response as white. For example, in the array for neuron type L+M-, strong and moderate activities are observed for neurons with receptive fields inside the red and yellow regions. The dark lines around each neuron type activities are shown only for the purpose of this figure and are not parts of the activities.

Figure 6: Cone activations to monochromatic spectral stimuli (Adapted from [12]).

and S − (L + M)+ neurons were not added to the model. Upon adding the latter neuron types, we expect to observe improvements in results.

In what follows, we will avoid using the terms red vs. green or blue vs. yellow for these neurons as usually misused. In fact, we would like to emphasize that the cones do not represent red, green, and blue, and the LGN neurons do not encode red vs. green or blue vs. yellow as normally considered. Specifically, consider the example of the red color. This color has wavelength at about 700 nm, while the peak for the L channel is at about 580 nm, as shown in Figure 6. As a result, the L channel does not encode red. The same applies to M and S channels.

Now, given that LMS channels do not encode red, green, and blue, the question is what hues do the model LGN neurons encode? To answer this question, we examine one of the model LGN neuron types specifically. Consider L-M+ neurons, for example. A closer look at Figure 6 reveals that L and M cones show sensitivity to slightly different wavelengths, and so, their responses do not differ much to various colors. It is, then, no wonder that the L and M channels shown in Figure 5 appear just slightly different. In single-opponent cells, this overlap plays an important role in the color these cells encode. These neurons, L-M+ cells, maximally fire when there are M signals and no L signals in their receptive fields. Such cases happen for colors with wavelengths in the range roughly about 450 nm to 550 nm. This range of wavelengths correspond to colors that look cyan-like, or bluish-green, in hue. Therefore, L-M+ cells encode cyan-like colors. It is, then, of no surprise that for a stimulus with red, green, blue, and yellow hues in four regions of the stimulus shown in Figure 5, L-M+ neurons show higher activations in regions with blue or green colors with relatively similar strength.

Neurons corresponding to regions with red and yellow hue show almost no activations. The story for L+M- and S+(L+M)- is more or less the same, except that L+M-
Table 1: The choice of cone weights for model LGN cells.

| LGN neuron types | L cone weight | M cone weight | S cone weight |
|------------------|---------------|---------------|--------------|
| L+M-             | 1             | -1            | 0            |
| L-M+             | -1            | 1             | 0            |
| S+(L+M)-         | -0.5          | -0.5          | 1            |

and S+(L+M-) neurons show selectivity to colors close to reddish and bluish hues respectively [13].

2.2 Model V1 and V2 cells

Local hue in V1, as suggested in [3] and [4], can be encoded by single-opponent cells. To obtain such a representation in model layers V1 and V2, the responses are determined by convolving input signals with a Gaussian kernel. Note that since single-opponency is implemented in model LGN layer, by simply convolving model LGN signals with a Gaussian kernel, we will also have single-opponency in model layers V1 and V2. The local hue responses of V1 and V2 were obtained by:

\[ R_{V1} = \phi(G(x,y,\sigma_{V1}) \ast R_{LGN}), \]  

\[ R_{V2} = \phi(G(x,y,\sigma_{V2}) \ast R_{V1}), \]  

where \( \phi \) is the linear rectifier in Eq. 2. In Eq. 4, substituting \( R_{LGN} \) with any of the three model LGN neuron type responses will result in a corresponding V1 neuron type. This applies to model V2 neurons. That is, in Eq. 5, substituting \( R_{V1} \) with each of the three model V1 neuron type responses will yield a similar model V2 neuron type. Therefore, there will be three neuron types in layers V1 and V2 corresponding to L+M-, L-M+, and S+(L+M)-.

The size of the Gaussian kernels for each of these neurons simply determines their receptive field sizes. In our implementation, the receptive field size doubles from one layer to the next following a similar observations in the ventral stream [10].

2.3 Model V4 cells.

We modeled V4 neurons representing local hue using a weighted sum of convolutions from the three model V2 neuron types. More specifically, V4 responses are computed as:

\[ R_{V4} = \phi(a_r(G(x,y,\sigma_{V4}) \ast R_{V2, r}) + a_g(G(x,y,\sigma_{V4}) \ast R_{V2, g}) + a_b(G(x,y,\sigma_{V4}) \ast R_{V2, b})), \]

where \( R_{V2, r}, R_{V2, g}, \) and \( R_{V2, b} \) are responses of V2 channels corresponding to L+M-, L-M+, and S+(L+M)- respectively. For notation simplicity, we are referring to these neuron types as \( r, g, \) and \( b, \) even though they do not correspond to red, green, and blue colors as discussed earlier. Again, \( \phi \) is the linear rectifier introduced in Eq. 2.

In Equation 6, the weights \( a_r, a_g, a_b \) determine the hue to which a model V4 neuron shows selectivity to. For example, for the setting \( a_r = 1, a_g = 0, a_b = 0, \) the V4 neurons show highest activity to reddish hues, as \( V2_r \) encodes this hue, while the setting \( a_r = 0, a_g = 1, a_b = 0 \) results in neurons selective to cyan-like hues.

In model layer V4, we implemented six different neuron types according to distinct hues: red, yellow, green, cyan, blue, and magenta. The chosen hues are 60 deg apart on the hue circle shown in Figure 7, with red at 0 deg. These hues were also identified on the V4 color map study [5]. From here on, we will refer to these neurons based upon their selectivity. For example, model V4 red or model V4 cyan neurons.

The weights used for each of these neuron types are shown in Table 2. These weights were set subjectively according to selectivity of each of V2 neuron type. For example, Yellow takes an equal amount of L+M- and L-M+ signals. But, since L-M+ shows selectivity to bluish-green colors, the bluish signal should be cancelled out. In Figure 5, at the V4 layer, from left to right, the neurons selective to red, yellow, green, cyan, blue, and magenta are shown. As expected, model V4 magenta neurons, for instance, show activations across both red and blue regions of the stimulus.

3 Results

In this section, we explain two sets of experiments performed on our model. First, we study the activations of model V4 neurons to various hues and make a comparison...
with biological V4 neurons. Second, we show that given the model V4 activations, any hue in the HSL space can be reconstructed.

### 3.1 Model V4 Selectivities

In this experiment, in order to test the effectiveness of our approach for modeling local hues, we examined the peak selectivity of each hue-selective neuron in layer V4. For this purpose, we sampled the hue dimension of the HSL space. We keep saturation and lightness values constant for this purpose, we sampled the hue dimension of the HSL space. We keep saturation and lightness values constant and set to 1 and 0.5 respectively. Our sampling consists of 60 different hues in the range of [0,360) degrees, separated by 6 degrees.

We present each of these 60 hues to the model and record the activities of model V4 neurons. Plots in Figure 8 show model V4 neuron activities to each of the sampled hues. In each plot, the circular dimension represents the hue, with red at 0 deg, and the radial dimension represents the response level of the neuron. These plots, for all model V4 neurons, show a peak of activity at their selectivity. The activities then start to diminish as the hues become more different from their selectivities. At the most distant hue, the hue 180 degrees apart from their selectivity, these neurons show almost no or close to zero activities.

Aside from the red neuron, which has a smooth curve, other plots show some irregularities. As described earlier, the single-opponent cells in V1 and V2 layers do not encode pure red, green, and blue colors and their transformation to the hue dimension might not be uniform. Therefore, when plotting activations along the hue dimension, such irregularities appear.

In Figure 9, we depicted our model with some stimuli for qualitative evaluation of the model. This experiment and its results illustrate that the model V4 neurons show selectivities to local hues, similar to those patches observed in [5]. In their study, Li et al. [5] found a correlation between the hue distances and the cortical distance of activated patches in each cluster. Figure 10 depicts three plots from [5], which show the cortical distances of the activated patches as a function of hue distances for three different clusters. In these plots, the hue distances vary between 0 and 5 as they first convert each hue to a number in the range [0,5], with 0 for magenta, 1 for red, and so on, according to the sequence ordering of patches witnessed in clusters. Then, the hue distances are computed as the difference of these values assigned. In this scheme of representation for hues, magenta and blue are two very distant hues with distance equal to 5, even though these hues are only 60 deg apart on the hue circle as shown in Figure 7. Moreover, magenta and green hues that are 180 deg apart are at hue distance equal to 3 in this form of representation. In short, their representation of hues does not capture the true distance of hues on the hue circle.

In order to test for a similar relationship between hue distances and the pattern of activities of model V4 neurons, we tested our model with the stimulus shown in Figure 9(b). Unlike Li et al. [5], we represent each hue by its angle on the hue circle, with red starting at 0 deg. Therefore, the longest hue distance is 180 deg. As an instance, yellow and blue that are farthest away from each other on the hue circle have the hue distance of 180 deg. This representation, in contrast with that of Li [5], has the benefit of mapping similar hues to smaller distances. In this case, blue and magenta are only 60 deg apart.

In this experiment, we analyzed the correlation between hue distances on the hue circle and the distance of maximally activated hue-selective neurons in each map. Specifically, we expected to observe that as the hues shift on the presented hue circle stimulus, the maximum activation location in individual model hue-selective neuron maps shifts with a similar pattern and moving from one neuron type to another. For this purpose, we computed six pairs of the form (hue, maximum response location) for each of the six hue-selective neuron maps in model V4 layer. As a result, we had $\binom{6}{2} = 15$ differences computed between each two of such pairs. The plot in Figure 11 demonstrates the maximum activation distances as a function of hue distances and exhibits a clear correlation. The correlation coefficient was $r = 0.9696, p = 2.5 \times 10^{-9}$.

In conclusion, we observed that the hue selectivity and pattern of activities of our model V4 neurons resemble those of neurons in V4 of the visual system. Moreover, this experiment demonstrates that local hue modeling can be achieved by combining signals from single-opponent cells. In other words, the intermediary hues that model V4 neurons represent are simply obtained from the primary hues that single-opponent cells encode.
Figure 8: Model V4 neuron responses to hues sampled from the hue dimension in HSL space. The sampled hues are 6 degrees apart. In each plot, the angular dimension shows the hues, with red at 0 deg, and the radial dimension represents the response level of the neuron. Model V4 neurons from top to bottom and left to right: red, yellow, green, cyan, blue, and magenta.
Figure 9: Qualitative examples of the hierarchical model. First, the input image is converted into LMS channels. The channels are shown as L, M, and S, from left to right. Each square in the model layers represents a map of neurons of a single type, with the neuron type written next to it. The receptive field of each neuron in these arrays is centered at the corresponding pixel location. The neuron responses are shown in grayscale, with no response as black, and maximum response as white. The dark lines around each neuron type activities are shown only for the purpose of this figure and are not parts of the activities.

Figure 10: Cortical distance of activated patches as a function of hue distances in three clusters in V4 (plots adapted from [5]).
Figure 11: Correlation analysis between the hue distances and maximum activation distances in each hue-selective map in model layer V4. The hue distances are in degrees and the activation distances are in pixels. Each neuron-type map in the model is 256 $\times$ 256 pixels.

3.2 Hue Reconstruction

In their work, Li and colleagues [5] showed that in monkeys, any hue was represented by 1-4 patches. Moreover, they showed that different hues were encoded with different multipatch patterns. Then, they suggested that a combination of these activated patches can form a representation for the much larger space of physical colors.

Along this line, we show, through a few examples, that for a given hue, a linear combination of model V4 neurons can be learned and used for representing that particular hue. It is important to note that it would be impossible to learn weights for the infinitely many possible physical hues. Hence, we show only a few examples here. However, our experiment is an instance of the possible mechanism for color representation suggested by Li et al. [5].

In this experiment, for a given hue value, we independently sampled the saturation and lightness dimensions at 500 points. The samples were uniformly distributed along each dimension. As a result, we have 500 colors of the same hue. The goal is to compute a linear combination of model V4 neurons, which can reconstruct the groundtruth hue.

The hues in this experiment were represented as a number in the [0, 2$\pi$] range. For numerical reasons, red is represented as 2$\pi$, not 0. Using the “stepwiselm” function in MATLAB (MathWorks), we performed a stepwise linear regression on the sampled colors. The choice of stepwise linear regression was made for the following reason. Model V4 neurons are not independent and therefore, the activities of these neurons used for learning are at times highly correlated. For example, magenta is highly correlated with blue with a correlation coefficient of approximately 0.98. This implies that a subset of these neurons is enough to describe the groundtruth hue. Stepwise linear regression serves this purpose. It takes one model V4 neuron at each step and considers adding it to or subtracting it from the model describing the data according to some criterion. A neuron will not be added to the model if it does not significantly improve the error term.

Table 3 shows some of the results for this experiment. Interestingly, in all cases, no more than three neuron types were selected, even though no such constraint was imposed. That is, the stepwise linear regression algorithm found that three types of neurons are enough to model the data. Moreover, the combination of the selected model V4 neurons spans the RGB space. As an example, in the case of hue at 360 deg, which corresponds to red, the set of selected neurons are blue, magenta, and red. Even though the weight for blue is relatively higher than that of red, the negative weight of magenta cancels it out.

In the yellow example, the only three neuron types are red, green, and yellow. The strong contribution of red neuron is somewhat canceled out with the negative contribution from the green neuron.

The last row in Table 3 is most insightful. It presents the weights for a hue in equal distance from blue (240 deg) and magenta (300 deg). The weights for this example seem counter-intuitive as it includes cyan with positive contribution and blue with negative. In addition, magenta is absent from this model. However counterintuitive the weights seem, they start to make sense when one considers the hue circle depicted in Figure 7 as described next. The hue at 270 deg, at first, can be seen as one between blue (240 deg) and magenta (300 deg). However, careful scrutiny of the hue circle reveals that this hue at 270 deg can also be considered between cyan (180 deg) and red (360 deg). Hence, this particular hue can be reconstructed by a combination of red and cyan neurons. The imbalance in the weights between red and cyan hues is to some degree canceled by the negative contribution of the blue neuron.

Once again, it must be stressed that this experiment was performed to examine the possibility of combinatorial representation mechanisms and a thorough investigation of this mechanism in the computational sense is left for future work. The examples shown here attest to the fact that intermediary hues encoded by model V4 neurons can indeed span the massive space of physical hues and are enough for reconstructing any arbitrary hue from this space.

4 Discussion

In this work, we introduced a hierarchical model for local hue representation. This biologically plausible model demonstrates that a network of single-opponent and hue-
Table 3: The choice of weights for model V4 cells used for hue reconstruction in a few example hues.

| Groundtruth hue (deg) | Model V4 neuron | RMS error |
|-----------------------|-----------------|-----------|
|                       | Red  | Yellow | Green | Cyan | Blue  | Magenta |       |
| red (360)             | 3.9356 | 0      | 0     | 0    | 5.3354 | -4.2718 | 0.0165 |
| Yellow (60)           | 2.0205 | 0.8326 | -0.4966 | 0    | 0    | 0    | 0.0027 |
| blue-magenta (270)    | 1.0074 | 0      | 0     | 1.6917 | -0.1153 | 0    | 9.4 × 10^{-6} |

selective neurons can achieve this purpose. We suggested a computational model for neurons resembling those in LGN, V1, V2, and V4. Through single-opponent mechanisms, we implemented L+M-, L-M+, and S+(L+M)-neurons in LGN, V1, and V2. Hue-sensitive neurons in V4 were obtained by input from these three neuron types. To our knowledge, this is the first study suggesting a computational model for color representation in a hierarchical framework of neurons up to and including V4. Our experimental results demonstrated that hue selectivity for model V4 neurons similar to that of neurons in layer V4 of the visual system was successfully achieved. In addition, our observations from the hue reconstruction experiment clearly confirmed the possibility of reconstructing the whole hue space using a combination of the hue-selective neurons in the model V4 layer. How this is achieved in the brain, for the infinitely many possible hues, remains to be investigated.

In future, we would like to extend the model to encode saturation and lightness. Moreover, we would like to address the problem of learning weights from V2 to V4. Finally, the experiment on hue reconstruction was performed with a simple linear regression model. A more sophisticated learning algorithm might result in more insightful weights. This experiment can be more extensively examined in future.

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References

[1] G. Bradski, “The OpenCV Library,” Dr. Dobb’s Journal of Software Tools, 2000.

[2] R. C. Reid and R. M. Shapley, “Space and time maps of cone photoreceptor signals in macaque lateral geniculate nucleus,” Journal of Neuroscience, vol. 22, no. 14, pp. 6158–6175, 2002. [Online]. Available: http://www.jneurosci.org/content/22/14/6158

[3] R. Shapley and M. Hawken, “Neural mechanisms for color perception in the primary visual cortex,” Current opinion in neurobiology, vol. 12, no. 4, pp. 426–432, 2002.

[4] E. N. Johnson, M. J. Hawken, and R. Shapley, “Cone inputs in macaque primary visual cortex,” Journal of Neurophysiology, vol. 91, no. 6, pp. 2501–2514, 2004.

[5] M. Li, F. Liu, M. Juusola, and S. Tang, “Perceptual color map in macaque visual area v4,” Journal of Neuroscience, vol. 34, no. 1, pp. 202–217, 2014.

[6] K. Yang, S. Gao, C. Li, and Y. Li, “Efficient color boundary detection with color-opponent mechanisms,” in Proceedings of the IEEE Conference on Computer Vision and Pattern Recognition, 2013, pp. 2810–2817.

[7] J. Zhang, Y. Barhomi, and T. Serre, “A new biologically inspired color image descriptor,” Computer vision–ECCV 2012, pp. 312–324, 2012.

[8] J. B. D. Paula, “Converting rgb images to lms cone activations,” Department of Computer Sciences, The University of Texas at Austin, Tech. Rep., 2006, technical Report 06-49. [Online]. Available: http://nn.cs.utexas.edu/?depaula:utestr06-49

[9] A. L. Rothenstein, A. Zaharescu, and J. K. Tsotsos, TarzaNN : A General Purpose Neural Network Simulator for Visual Attention Modeling. Berlin, Heidelberg: Springer Berlin Heidelberg, 2005, pp. 159–167.

[10] J. Freeman and E. P. Simoncelli, “Metamers of the ventral stream,” Nature neuroscience, vol. 14, no. 9, pp. 1195–1201, 2011.

[11] R. Shapley and M. J. Hawken, “Color in the cortex: single- and double-opponent cells,” Vision research, vol. 51, no. 7, pp. 701–717, 2011.

[12] A. Stockman and L. T. Sharpe, “The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype,” Vision research, vol. 40, no. 13, pp. 1711–1737, 2000.
[13] I. Abramov and J. Gordon, “Color appearance: On seeing red-or yellow, or green, or blue,” *Annual Review of Psychology*, vol. 45, no. 1, pp. 451–485, 1994.