Efficiency of Information Coding in Various L/M Retinal Cone Ratios

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ABSTRACT

Previous evidence has shown that the number of L and M cones in retina varies significantly between subjects. However, it is not clear how the variation of L/M ratio changes the behavioral performance of the subject. A model of transformation of data from retina to visual cortex for evaluation of various L/M cones ratios is presented. While L/M cone ratios close to 1 brings the best performance for one of postreceptoral (magnocellular) channels, we showed that the performance in the second channel (parvocells) will improve when the ratio furthers away from 1. Effects of different ratios of S were also explored.

1. Introduction

Three types of cones exist in human retina with different spectral sensitivities. L (sensitive to Long wavelengths), M (Medium), and S (Short) cones form the input for the postreceptoral pathways that transfer information from retina to the primary visual cortex via lateral geniculate nucleus. Postreceptoral pathways include three types of cells; large and fast magnocells which transfer the luminance information, delicate and slow parvocells that compare the inputs of L and M cones, and less frequent koniocells that heavily rely on the input of S cones and its comparison with the other two types of cones.

Behavioral, structural, and computational studies have furthered our understanding of how the cones and postreceptoral pathways are arranged. Magnocells collect outputs of all three types of cones to form a channel that conveys a gray-scale (i.e. luminance) image. Parvocells differentiate between inputs of L and M cones; thus conveying a ratio of a reddish vs. a greenish color. Koniocells, on the other hand, compare the output of S cones with two other types of cones and therefore, discriminate yellow-greenish hue from a bluish color. Computational models show that the most efficient way of coding information from retina to visual cortex is to have the same three pathways. Principal component analysis of the natural scenes, a method to estimate the minimum bits for transferring data, defines the first component as a sum of the inputs from all three cones (similar to magnocells, the most numerous postreceptoral cells), the second component as a subtraction of L from M (similar to parvocells), and the third component as the subtraction of S cones from the average of L and M cones (similar to koniocells). We use three terms of

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Luminance (Lum), Red-Green (RG), and Blue-Yellow (BY) for three post-receptoral channels magno, parvo and konio cells respectively.

However, direct imaging techniques of human retina as well as functional tests and post-mortem analysis have showed that the ratios of L to M cones vary significantly among different subjects. A behavioral estimate of L/M cone ratio suggested a range of 0.6 to very high (near deuteranopic, i.e. no M cone) ratio[1]. A postmortem analysis of retina of 23 male subjects showed a variation of L/M cone ratios of 0.8 to 3[2], and a later expansion of the study of 100 males showed a wider range of 0.8 to 9.7. In 1999, a report of direct retinal imaging in two subjects showed an L/M ratio of 1.15 and 3.79[3].

The variance in the L/M ratio begs the question whether the input to each of postreceptoral pathways varies based on the ratio of the cones. In other words, if the L/M ratio is, for example, 2/1 in a person, does magnocellular pathway receive input from an average of two Ls and one M, or it remains constant and a summation of one L and one M? The latter does not make sense since it would be a waste of resources for the organism, and the speculation is that during the critical period, when the 'pruning' of neurons happens, extra unused cones should vanish.

Yet, another possibility might be the usage of a fixed ratio for one of the pathways for most of the subjects, and a different ratio for another pathway. A model then would be, for example, 1*L+1*M+1*S for the magnocells, while the parvocells may use the input by various ratios in different subjects, i.e. x*L-y*M (where x/y would be the ratio of L/M). We have evaluated the effect of various coding on the transfer of information and their efficacy.

2. Methods

We used a publicly available color calibrated database from McGill University[4]. These images are from natural scenes taken by a calibrated camera and have been divided into several categories such as animals, landscape, snow, fruits and flowers. RGB values of each pixel of each image were converted to a model of LMS cone responses (for details of this conversion, please see[5]). In summary, the scenes were photographed with a Nikon CoolPix-7500 digital camera. The cameras were calibrated as follows. Each one of a set of grey Munsell papers was illuminated by an incandescent light with a constant-DC power, and photographed. Additionally, the luminance of the light reflected from each paper was measured with a Topcon SR-1 spectroradiometer. The average R, G, and B pixel values were plotted against the corresponding measured luminance, and fitted with the following function: L = a(bs +1), where L is luminance, s is the pixel level value obtained for each of the camera sensors (R, G, and B) and b a constant that determines the slope of the curve. In addition, a white target was photographed through a series of narrowband optical interference filters from 400 to 700 nm at 10nm intervals. Each R, G and B value was recorded, gamma-corrected and used to construct a spectral sensitivity function for each sensor, which was then normalized to produce equal responses of to a flat-spectrum light.

In order to model the three post-receptoral channel responses to images of natural scenes one needs to use a color space. The most commonly used color space is a version of the one developed by MacLeod and Boynton and later by Derrington and colleagues[6,7]. In the cone-contrast version each cone's response is normalized to that of the cone response to the stimulus background, e.g. $\Delta L/L_b$, $\Delta M/M_b$, $\Delta S/S_b$, as the background cone contrast is assumed to determine the state of cone adaptation. While this is a reasonable assumption for briefly presented stimuli such as gratings, or low contrast patches, it is arguably inappropriate for natural scenes which tend to be of high contrast and for which cone adaptation is likely determined locally rather than by the average of the scene as a whole. Another, logarithmic-based version suggested by Ruderman Cronin & Chiao[8], transforms cone responses to a logarithmic space and then normalizes each post-receptoral channel response by the mean (log) value over the image. The logarithmic transform models a transducer function that produces Weber's law for increment thresholds[9], and removes pure-luminance shading and shadows from the red-green channel. The three channels were modeled as equation 1:

$$\begin{aligned} L_C &= \log L - \overline{\log L} \\ M_C &= \log M - \overline{\log M} \\ S_C &= \log S - \overline{\log S} \end{aligned}$$

And then

$$\begin{cases} Lum = L_C + M_C + S_C \\ RG = L_C - M_C \\ BY = \dfrac{L_C + M_C}{2} - S_C \end{cases}$$

Equation 1

However, we wanted to evaluate the effect of the ratios of L/M. Therefore, we added coefficients for each of the cone cells:

$$Lum = xL_C + yM_C + zS_C$$
$$RG = xL_C - yM_C$$
$$BY = \frac{xL_C + yM_C}{x + y} - zS_C$$

Where x, y and z are the ratios of the three cones.

We used a series of consequent values for each of coefficients x (from 1 to 14) and y (from 1 to 10); i.e. (x=1,2,3,…,14, y=1,2,3,…,10), or in other words, we created an array of (x,y)=(1,10),(1,9),…,(1,1),(2,1),(3, 1),…,(14,1). We used higher values for x because previous studies have reported ratios of L to M from 13 to 0.4. In this sequence, in fact, we covered a range of L/M ratio of 14 (14:1) to 0.1 (1/10). For the first step, we used a zero value for S cone coefficient to assess the main aim of the research, the L/M cone ratio effect.

Principle Component Analysis (PCA) is a mathematical method which uses orthogonal transformation of data to 'de-correlate' the values. This would result in the highest possible variance in the 'first axis', and can be used, for example, for dimension reduction or compression of data. Previous studies have shown that the three principle components of data of natural scenes closely match the way the post-receptoral channels convey information 8. After mean subtraction in PCA, a minimum mean square error is calculated and the first axis will be measured based on that.

Then similar to principle component analysis, the minimum standard error (MSE) of the data points from 3 axes (Lum, RG, BY) was calculated jointly. To be precise, first the MSE of the data points from the luminance axes were found and then all the data point space were projected into the plane witch composed from conjunction of the BY & RG axes. Finally, the quantity of the MSE from BY & RG axes were measured using coordination of the mapped data points.

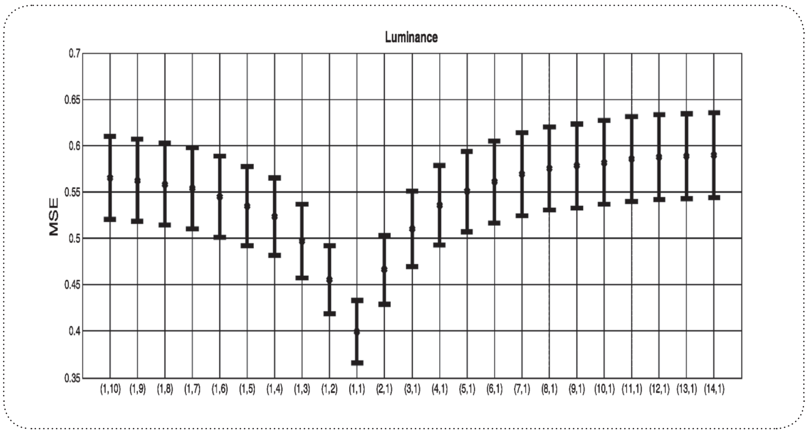

Figure 1. MSE fromLuminance Axis with standard errorsfor consecutive values of x and y (x axis).

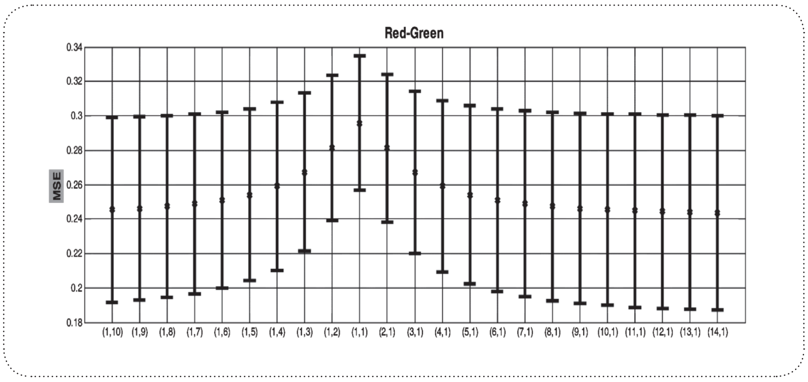

Figure 2. MSE from RG Axis with standard errors for consecutive values of x and y (x axis).

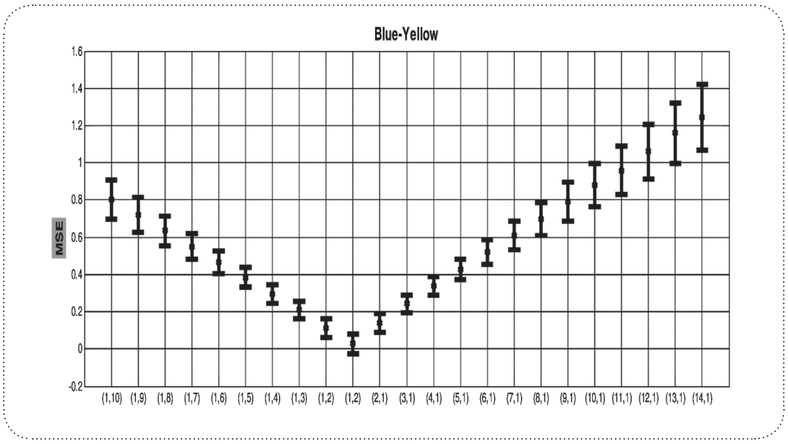

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Figure 3. MSE fromBY Axis with standard errorsfor consecutive values of x and y (x axis).

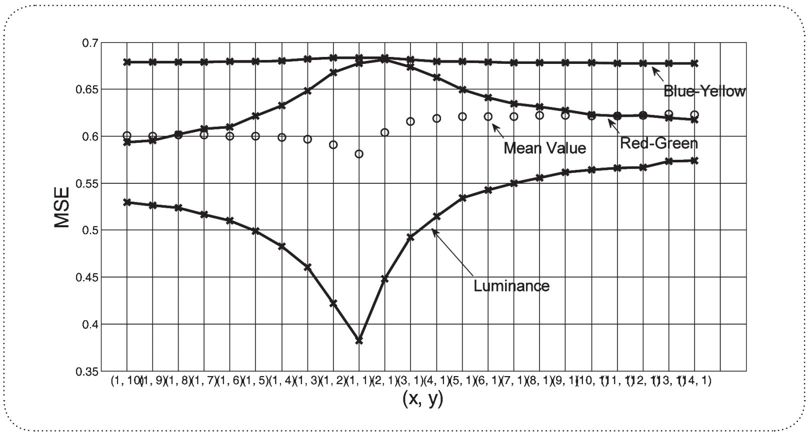

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Figure 4. Summary of MSE values on the same scale for all three axis

3. Results

We also used the same caluclaution for different values of z (x=1,2,3,…,14),(y=1,2,3,…,10) and z=(1,0.9,0.5,0.1,0.01). Therefore, for each value of z, we had (x,y)=(1,10),(1,9),…,(1,1),(2,1),(3,1),…,(14,1. The results are plotted in figure 5-7.

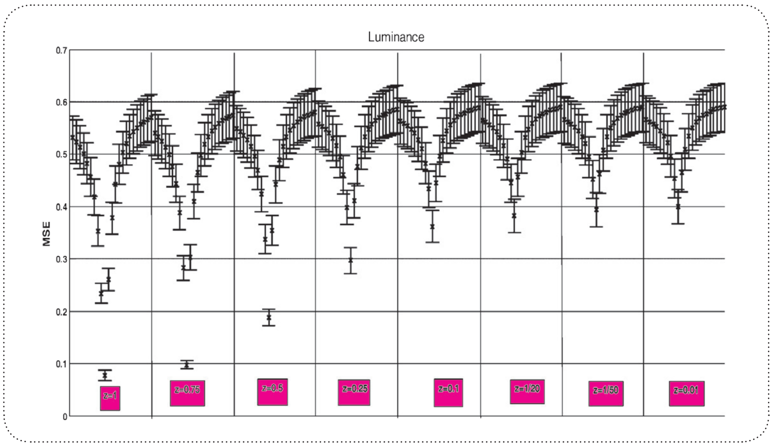

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Figure 5. MSE fordifferent x and y values in the luminance channel separated by different z values.

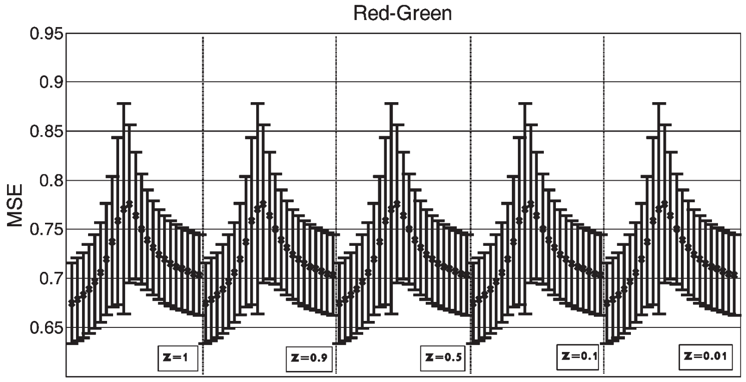

Figure 6. MSE for different x and y values in the RG channel separated by different z values.

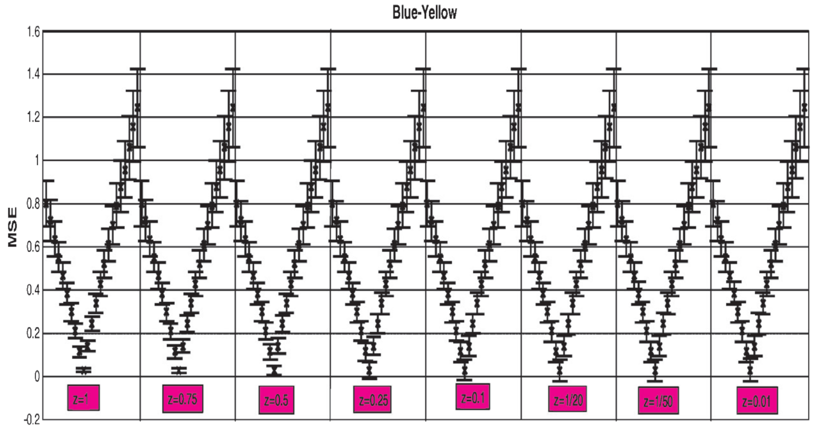

Figure 7. MSE for different x and y values in the BY channel separated by different z values.

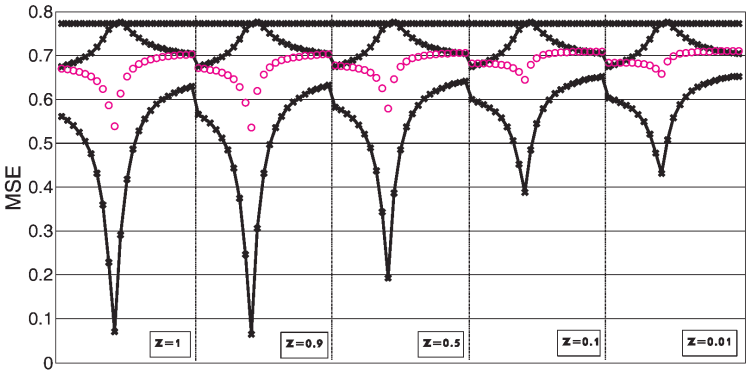

Figure 8. Summary of MSE in all three AXES, on the same scale.

In the final part of our experiment, we measured the effect of changes in z (S cone ratio), while keeping the x and y (L and M ratios) fixed. The MSEs are measured in luminance channel. The results are shown in figure 9.

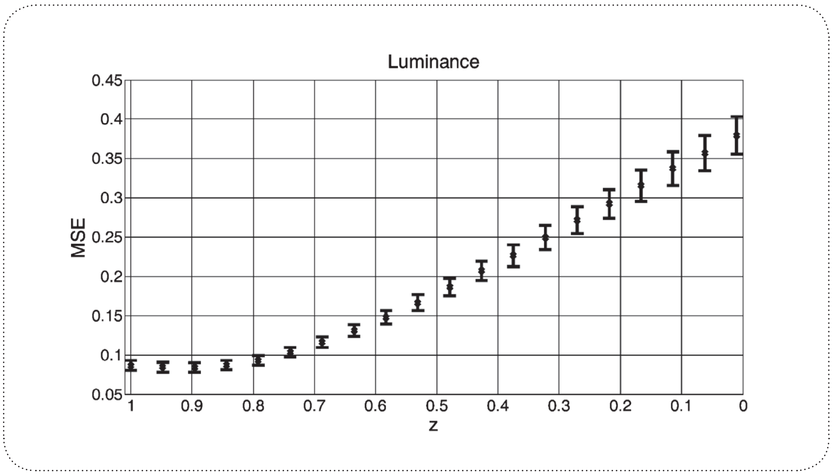

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Figure 9. The Mse Will Increase If The L And M Ratio Are Fixed While The Ratio Of S Cone Increases.

4. Discussion

Retinal L/M ratio varies significantly in humans. We showed that the changes in L/M ratio make one of the axis less effective, while the other one more efficient, and therefore, make the effects of changes less variable in the post-receptoral channels. With changes in L/M ratio far away from 1, the efficiency of luminance channel (magnocells) would be less efficient, and the parvo cells change in the other directions.

One of the possibilities of the structure of postrecpetoral channels is that they do not use all the retinal cones available for their input. In other words, while the ratio of L/M may vary, for example for parvocells, the ratio for magnocells may remain 1/1 in humans. This possibility, though not very plausible, may exist. In this case, the ratio of L/M will affect only the parvocells and its sensitivity, while the magnocells may remain similar in most of the subjects.

To test this model, the white point may vary for subjects that their red-green contrast balance for isoluminant point is different. Since the isoluminant point can be used to measure the L/M ratio of the parvocells, if the same ratio could be applied to magnocells, we would expect that the white point for these subjects vary as well. The white point should lean toward red (L/M ratio >1) or green (L/M ratio<1).

In summary, the variation in L/M cone ratio would lead to lower performance in one post-receptoral channel, while increases the efficiency in the other channels.

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