Ideal Illuminants for Rod /L-Cone Color

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ABSTRACT

Humans see multicolor complex images with illuminants that have very low amounts of 400 to 580nm light when there is enough long-wave light greater than 590nm. Interactions between rods and long-wave (L) cones generate these colors. They are observed when there is insufficient light for a threshold response from M- and S-cones. This paper measures the spectral emission of a wood fire and a wax candle and it compares these low-color temperature spectral radiant exitances with the sensitivities of rods and long-wave cones. The paper reviews some of the literature on the evolution of human cone pigments and the early use of fire by hominids.

1.0 INTRODUCTION

Experiments measuring the human threshold action spectra have lead to the Scotopic and Photopic Luminosity curve standards[1] (Figure 1). The Scotopic curve is generated by rod shaped receptors in the retina. They are 100 times more sensitive to 546 nm light than cone shaped sensors (Photopic curve).[2]

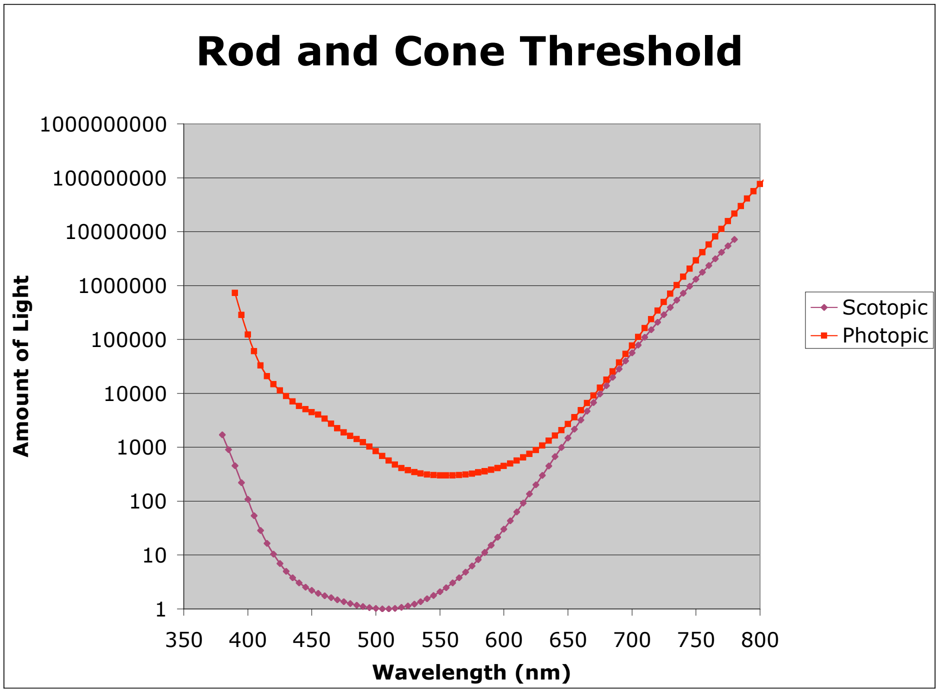

Figure 1 plots the reciprocal of the photopic and scotopic luminosity curves. It plots the amount of light verses wavelength to obtain a threshold response. These curves are usually plotted as sensitivity (1/threshold). Humans are most sensitive to 507nm light at absolute threshold for detection by rods. The photopic standard associated with cone vision is most sensitive at 555nm. The spacing of the two curves is based on experiments that measured the absolute threshold for narrow-band 546nm light and the rod-cone break in the dark-adaptation curve.[2] This data show that the rods are 100 times more sensitive to 546nm light than are the cones.

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Experiments using colorful displays illuminated with narrow-band lights have shown that observers report multicolor appearances in near scotopic threshold conditions.[3] Specifically, these conditions are above absolute cone threshold for 656nm light and above absolute rod threshold for 510nm light.[4] The 510nm light was more than 1000 times below radiance required for M- and S-cone responses. This fact was demonstrated by study of a large number of the different rod and cone characteristics. The list of characteristic studied was: the rod-cone break in dark-adaptation curves; the change of image sharpness; the change of color appearances; the change of the flicker-fusion frequency rate; and the change of the Stiles-Crawford ratio; as well as action spectra measurements using *best color balance* for a criterion. All these characteristics showed the same radiance level for transition from rod response to cone response. Complex color images were observed below this rod-cone transition. In some circumstances, color was seen with radiances 1/1000th that required for M- and S-cone responses.[4,5]

The action spectra, mentioned above, were measured using a dual-image monochromators to illuminate and combine a pair of black and white continuous-tone transparencies. These transparencies were red and green color separation photographs of a navel orange on a multicolored array of papers. The device presented the combined images in Maxwellian view. The long-wave record (**Lrecord**) was illuminated with 656nm light with fixed radiances. The middle-wave record (**Mrecord**) was illuminated with variable wavelengths (420 through 610nm) and variable intensities. In a control, the experimenter shut off the 656nm light and asked the observer to adjust the radiance of the **Mrecord** until he could report seeing very faint forms. The experimenter illuminated that record with 10 different wavelengths and the observer set the radiance for each for minimal form threshold. The data fit the shape of the scotopic luminosity curve, showing that rods were generating the minimal-form threshold response.[4]

In a color threshold experiment, the 656nm radiance was set just above L-cone threshold. The experimenter set the **Mrecord** wavelength and the observer selected the radiance so that the image had the best color balance (not too warm and not too cool). The action spectra for threshold color fit the shape of the scotopic luminosity curve, showing that rods were controlling the color balance of the color threshold image.

The experimenter increased the 656nm radiance by a factor of 13 and repeated the experiment. The best color balance required more illumination for the variable wavelengths illuminating the **Mrecord**. The measured action spectra again fit the scotopic luminosity curve.

In total, the experiment used 7 different radiances for 656nm light. Four of the resulting curves showed that the data fit the scotopic curve. Rods determined the amount of 420 to 610nm light for *best color balance*. The three curves with the highest 656nm radiances had action spectra that did not fit the scotopic curve. The radiances chosen for these *best color balance* judgments were all higher than the rod-cone break in dark-adaptation curves. For these light levels, M- and S-cones determined the *best color balance*. Since the observers' task was simply to adjust the image for color, and since the results matched the scotopic sensitivity function over a range of 1000 to 1, it provides evidence that rods are involved in color appearances at low light levels, rich in long-wave light.[4]

2.0 TRICROMACY FROM FOUR RECEPTOR SYSTEMS

At low levels of moonlight humans have a monochromatic, scotopic visual system. If we illuminate an array of colored papers below all three cone thresholds, all papers appear different shades of gray. With colored papers, changing the wavelength of illumination will change the lightness of colored papers, because the papers have different reflectances for different wavelengths. Alternatively, if we vary the wavelength of illumination on an array of black, gray and white papers, their reflectances are constant for all wavelengths. Here, the appearances below cone threshold vary in overall intensity tracking the scotopic luminosity curve. If one adjusts for the sensitivity at each wavelength, then the appearance of a gray paper is the same, regardless of wavelength.[3]

At higher levels, when three cones and rods are all above threshold, we have trichromatic color vision. When a low-level illuminant has greater long-wave content rod/Lcone multicolor images are observed. Image monochromator experiments have shown that substituting different wavelengths that excite only the rods cause no change in color appearance of the rod/Lcone color images. The experiment used a dual-beam image monochromator. The long-wave channel used a black and white *red-separation* record with constant 656nm illumination. The short-wave channel used a black and white *green-separation* record with variable *wavelength & intensity* illumination. When the long wave channel was off, the intensity of each wavelength was adjusted to maintain the same appearance. Wavelengths far from the peak of rod sensitivity require higher radiances. The result was that varying the short-wave *wavelength & intensity* combinations generated constant colorless rod images. Multicolor images were observed when the physically constant long-wave record was combined with the variable *wavelength & intensity* middle-wave record. In all cases, each complex image was constant. All colors were invariant despite changes in shortwave-wavelengths from 420 to 570nm.[3]

The interesting question is whether four active color receptors are trichromatic or tetrachromatic. What do the colors from the above experiment look like? Are they different colors from those usually observed? A further experiment used a second dual image monochromator with identical transparencies. The second image had increased radiances (above cone threshold) for both long- and short-wave records. The observer's task was to select the wavelength above cone threshold that matched the complex color image from rod/Lcone image. The result was 495nm. This wavelength falls between the M- and S-cone fundamental peaks indicating that the rod signal is shared with both M- and S-color channels. If the observer had selected 445nm that would indicate that the rods sent signals to only the S-color channel. Human color is trichromatic, despite the fact that we have four active color receptors.

3.0 IDEAL ILLUMINANTS FOR ROD/LCONE COLOR

This paper reports on measurements of the spectra emission of firelight as an interesting light source with increasing long-wave light emissions with longer wavelengths. Is firelight a suitable illuminant for Rod/Lcone interactions?

3.1 Wood Flame

We measured the spectral emission of a wood fire using a PhotoResearch PR650 SpectraScan® meter. The meter recorded the spectra of flames in fires. The meter measures light with a field of view of 1 degree. Under these conditions the exposure time is about 200ms to measure the 380 to 780nm spectral radiances. Figure 2 plots 18 measurements of flames in a wood fire in a fireplace. (Wood Fire All).

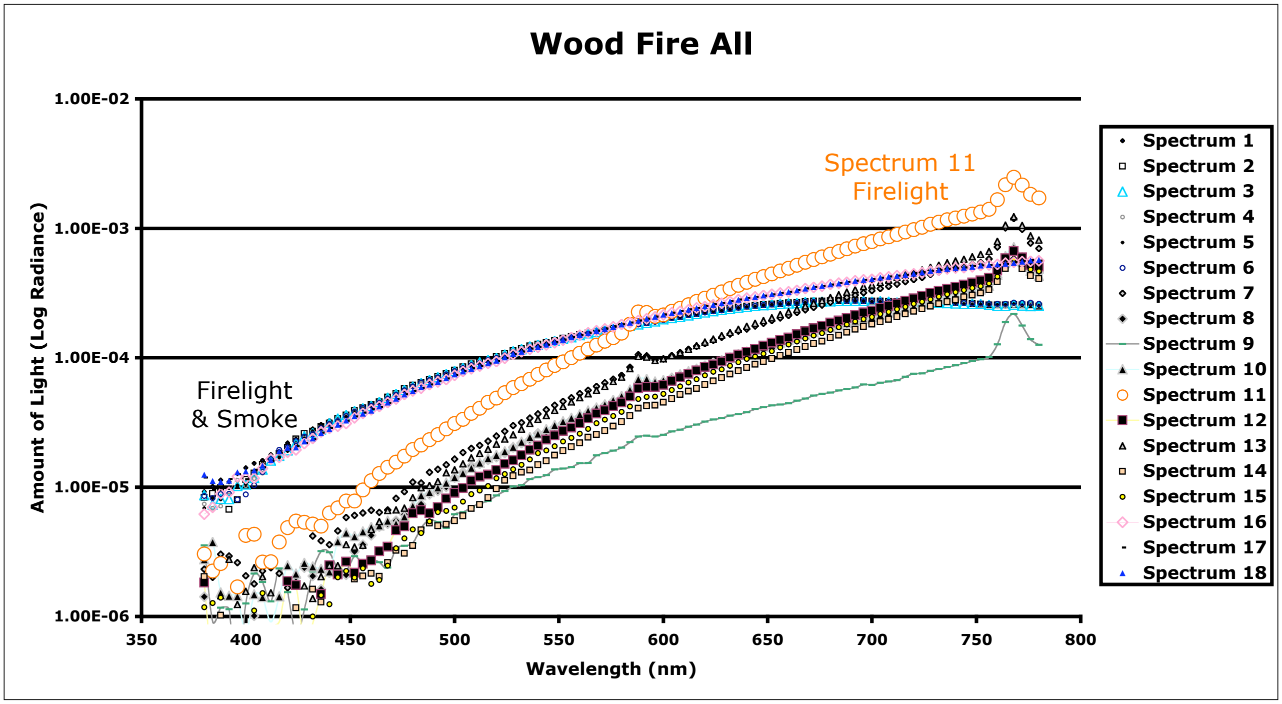

Figure 2 plots radiance vs. wavelength for 18 measurements of the spectral emission of a wood fire. The data falls into three categories. First, Spectrum 11 data had the highest amount of long-wave light and represents the best measurement of flame. Second, Series 1, 2, 3, 4, 5, 6, 16, 17, 18 emit more short-wave and less long-wave light than the other measurements. These spectra were measurements of fire and smoke. Third, the rest of the spectra were various mixtures of smoke and flame because their spectra are intermediate.

The flames from a wood fire are variable in intensity and show small shifts in wavelength spectra. Smoke made by the fire is another source of variability. The first six measurements were taken as the fire was growing was consistent with each other and slightly different from later measurements. Series 1, 2, 3, 4, 5, 6, 16, 17, and 18 show asymptotes above 650nm and are very consistent in radiance. The average of these curves is called *Wood Flame+Smoke*. The rest of the measurements showed increasing emissions with wavelengths greater than 650nm and greater variability in intensity. Series 11 data has the highest amount of long-wave light and appears to be the best measurement of smokeless flame (*Wood Flame*).

3.1 Candle Flame

Second sets of spectra were collected from flames from a wax candle. A candle flame is very steady in a quiet room and provides a much more constant smokeless flame than a wood fire. The average of these curves is called *Candle Flame*.

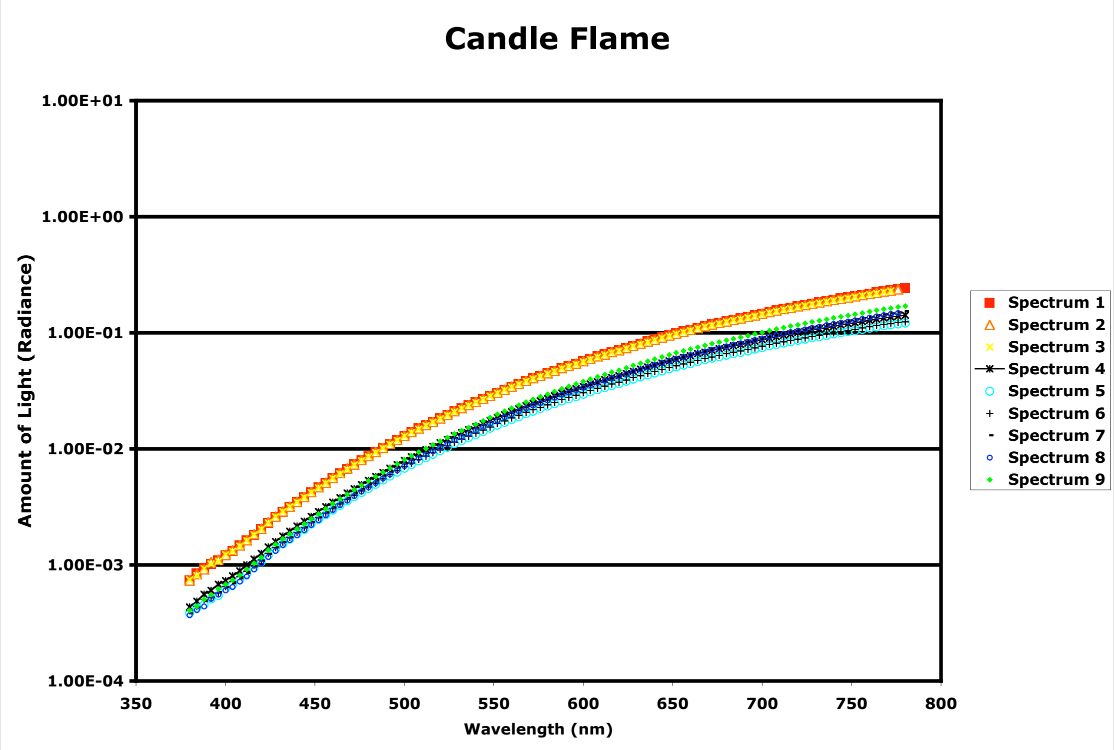

Figure 3 plots radiance vs. wavelength for 9 measurements of the spectral emission of a candle flame. These spectra are much more consistent than those of the wood fire. There are only slight variations in intensity and no visible smoke.

In order to estimate an equivalent color temperature for these flames we plotted their emission spectra on exitance curves for blackbody radiators.[6] Figure 4 plots the curves between 1000° K and 2000° K radiators. *Wood Fire Flame* has the lowest equivalent color temperature about 1700°K. *Candle Flame* is slightly higher fitting closely to 2000°K.

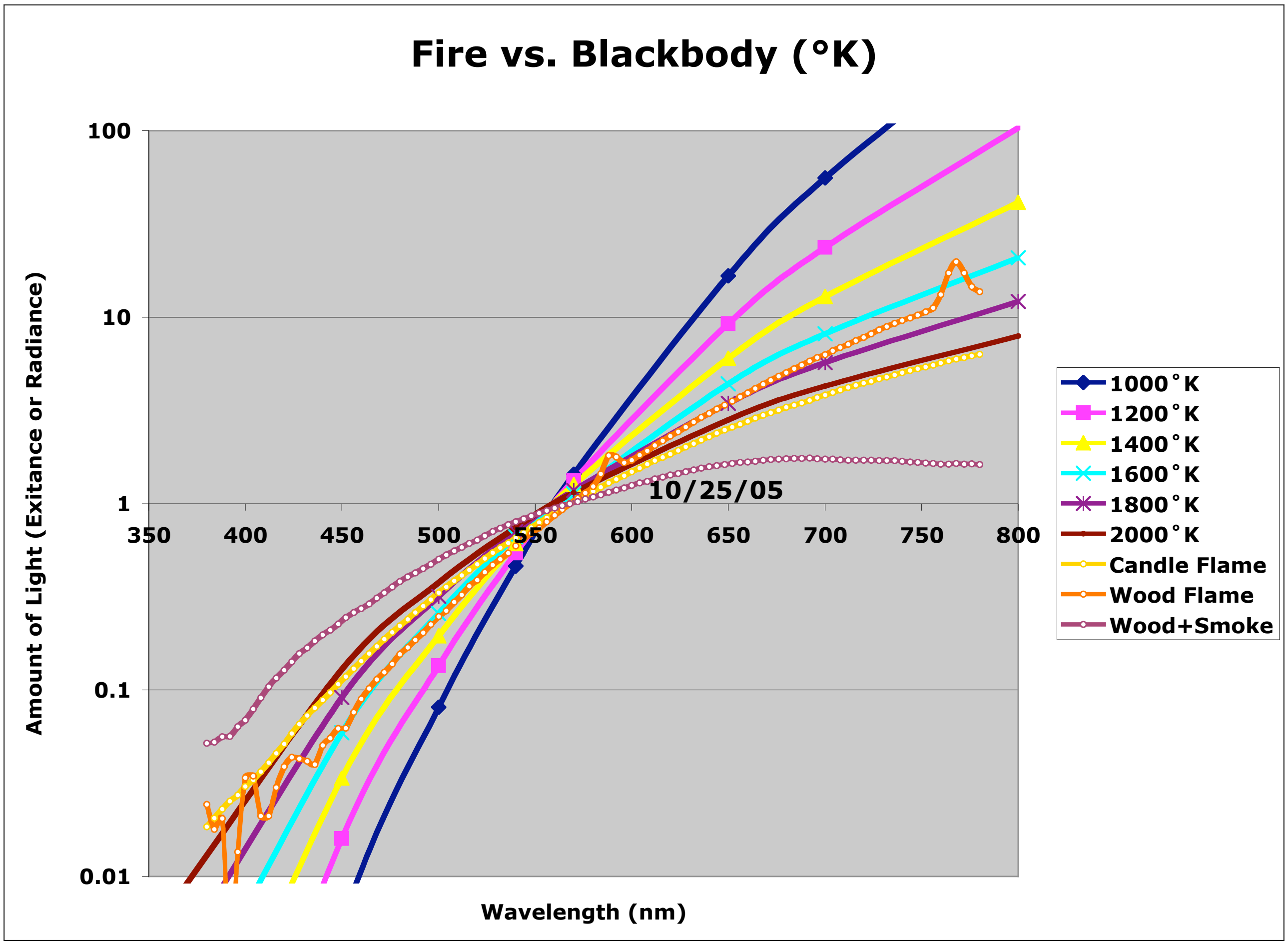

Figure 4 plots radiance vs. wavelength for the spectral emission of the *Candle Flame*, *Wood Flame*, *Wood Flame + Smoke* (white centers). The lines are the exitance for black body radiators at 1000° K, 1200° K, 1400° K, 1600° K, 1800° K, 2000° K (solid lines). The *Wood Flame* has the lowest equivalent color temperature, close to 1700° K. The *Candle Flame* is close to 2000°K. The *Wood Flame and Smoke* is greater than 2000°K

Figure 5 superimposes on the fire emission spectra the rod, L-, M-, S- cone sensitivity curves. Cone curves are 10° cone fundamentals from Stockman and Sharpe[7]. The *Wood Flame* and *LconeSen* were scaled to 1.0 at 568nm. The moonlight curve normalized to the Wood Flame at 507nm.

The relative sensitivities of L- and M- cone fundamentals were scaled so that (*LconeSen=1.76*MconeSen)*. Stockman and Sharpe described that the 1.76 factor gave the best fit (standard error = 0.05) to photopic luminosity curve, using the following equation.[7]

$$V_{\lambda} = 1.76 * LconeSens(\lambda) + MconeSens(\lambda)$$

Since their fundamentals describe the shape of the cone functions, they used the luminosity function to establish the relative sensitivities of L- and M-cone fundamentals. (In Figure 5 the S-cone fundamental is arbitrarily scaled to be the same as that for the M-cone.) S-cone fundamental does not contribute to the V_{λ}.[7]

Figure 5 also shows the spectral distribution of moonlight. We used a 1 degree PhotoResearch PR650 SpectraScan® meter described above. The data here is the average of 5 independent scans of the moon (filling the meters field of view) on a clear night August 17, 2005(Belmont). Moonlight is comparatively flat above 500nm compared to firelight. The two curves were normalized at 500nm, the peak of rod sensitivity. Firelight emits almost an order of magnitude more long-wave light than moonlight. Firelight can generate above-threshold images for the rods and long-wave cones, but is below threshold for M- and S- cones.

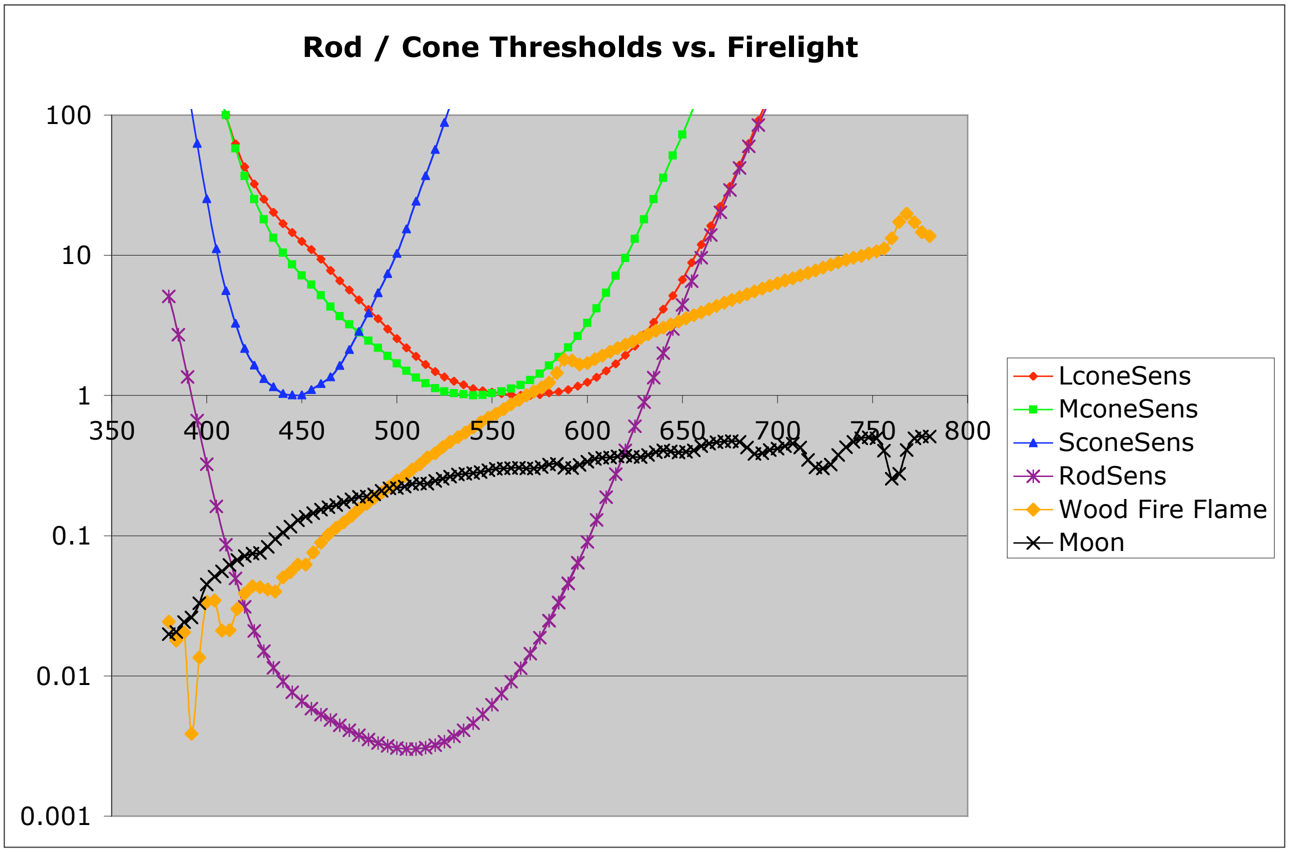

Figure 5 plots the reciprocal Long-, Middle, and Short-wave cone fundamentals from Stockman and Sharpe. In addition, it plots the reciprocal of the scotopic sensitivity for the spectral shape of rod threshold. The *LconeSen* and *The Wood Flame* measurements are normalized at 568nm. The Moon measurements were normalized to *Wood Flame* at 507 nm. *Wood Flame* has sufficient long-wave light to excite the L-cones. There is sufficient light below 550nm to excite the rods, but not the M- and S-cones. Firelight is an ideal illuminant for rod/cone color vision.

As shown in Figure 4, the *Wood Flame* measurements have the highest ratio of long- to short-wave light. Compared to sunlight, daylight, and moonlight it is much better illuminant for stimulating the rods and L-cones, without exciting the M- of S- cones. Figure 5 plots the *Wood Flame* spectra along with the amounts of light to reach rod and cone thresholds. *Wood* Flame will generate color images with amounts of light below M- and S-cone thresholds.

4.0 DISCUSSION

Opsin chemistry is found in species 600 million years old.[8] Trichromatic color vision is found in many species much earlier than primates.[9] Tim King's recent paper at Electronic Imaging[10] described how early mammalian color vision lacked red sensitivity. He reported that ancestors of human and Old-World monkeys developed a new long-wave cone pigment around 50 million years ago (Mya). Humans and Old-World Monkey have L- and M-wave sensitive cone pigments encoded by X-linked genes. New World monkeys possess only one X-linked and one autosomal cone gene.[11] The hypothesis is that a mutation duplicated the M-cone, X-linked gene after the Old World /New World lineage separated. Separate L and M wave X-linked photopigment sequences are found in Old World monkeys. Each gene then shows a separate lineage into Hominid and Cercopithecoid lineages (30Mya).[12] This is consistent with the idea that the duplication mutation occurred early in the evolution of old world primates.[13]

Genetic studies of marmoset, squirrel monkey and human compared sequences of the three polymorphic alleles at the X-linked color photopigment locus. These three alleles encode the two photopigments similar to those found in human L- and M-cones. These studies concluded that these different alleles in each species apparently have persisted more than 5 million years.[14]

On the other side of the coin, anthropologists have done extensive research on man's early use of fire. The anthropological estimates vary from 250,000 to 1.6 million years ago. S. R. James's review offers a conservative estimate between 300,000 and 250,000 years ago. He compiled data from 34 different archeological sites worldwide. The sites range from Africa and the Near East, to Europe and Asia. At St. Esteve-Janson in Europe archeologists found five different characteristics of controlled fire: 1) hearths, 2) charcoal, 3) fire-cracked rock, 4) reddened clay and 5) ash around the hearths.[15] L. G. Straus describes evidence in Africa between 300,000 and 200,000 years ago that hominids developed the cultural means controlling fire as a prerequisite for inhabiting glacial Western Europe.[16]

More recently, Bellomo cites evidence for 1.6-million-year old controlled fires. [17] Thermal and paleomagnetic data suggest that the reddened patches at Koobi Fora represent repeatedly used hearths. Based on crystalline melting in the earth, Rowlett and Bellomo gauged the temperature of the fires at around 400 °C. Bushfires normally burn at just 100 °C.[18] Bellomo also used archaeomagnetism, to show that hominids revisited Koobi Fora fires over a period of years. Heating causes iron in the soil to align with the earth's constantly wandering magnetic pole. Bellomo found that the sediments had a mix of slightly different magnetic orientations. He also found no evidence of cooking and argues that fire was at first used only for heat, light, and protection against predators. At Swartkrans, burned bones are associated with hominid artifacts at around 1.6 million years.[19] Brian Ludwig made an exhaustive analysis of flint artifacts and the debris of tool making. He inspected around 40,000 pieces collected from over 50 sites in Africa, covering the period from 2.5 million to less than 1 million years ago. He found characteristic signs of thermal alteration on many of the tools, dated later than 1.6 million years ago. After that date, thermal alteration occurred consistently across many sites, including the Olduvai.[18]

Wrangham et. al. reports that the African climate became increasingly dry in the lower Pliocene citing the work of Brain and Vrba. [20] They say that natural fires would have occurred with increasing frequency. Lightning strikes, volcanic activity, spontaneous combustion, and percussion sparks from rockfalls have been identified as likely sources of fire[21,22]. If campfires maintained over several years and heat altered tools are the signatures of 1.6 million years ago, what is the appropriate date for the first use of fire as illumination? Natural fires would have affected all animals, not just hominids, in that it destroyed habitats. How did fire affect food gathering in Africa? We should not restrict our thinking to hominids using a torch. We should also consider hunting, foraging and competing with other animals in the vicinity of uncontrolled natural fires.

There is a very large window in time between the mutation of opsin to improve long-wave sensitivity and hominid's controlled use of fire. The evidence of re-evolution of long-wave sensitivity is 50 to 30 Mya and the controlled use of fire in pits is 1.6 Mya. Nevertheless, the evolution of trichromatic cone vision from dichromatic requires three distinct system changes. One requirement is the mutation of opsin to change the wavelength sensitivity of the cone pigment. Another is the duplication of the M-cone gene to provide a third class of cone receptor. The third requirement is a re-wiring of the neural circuitry to be able to compare L-cone signals with M-cone signals. Identical processing of L-cone and M-cone signals would just mix spectral content, not provide a third dimension to color space. Sometime in between 30 and 2 Mya primates began to interact with natural fire. It remains to be seen whether the availability of natural fire could have influenced the evolution of color vision.

5.0 CONCLUSIONS

Wood flame light is equivalent to a black body radiator of about 1700°K. It is sufficiently rich in long-wave light to generate color vision at low light levels by stimulating the long-wave cones and rods. It remains a question whether natural fires influenced the evolution of long-wave cone sensitivity mechanisms in the ancestors of Old-World Monkeys and early hominids. Wood flame has the ideal spectral properties for seeing color at very low light levels.

6.0 ACKNOWLEDGEMENTS

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7.0 REFERENCES

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